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Intercontinental Migration of Neogene Amphicyonids (Mammalia, Carnivora): Appearance of the Eurasian Beardog *Ysengrinia* in North America

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ABSTRACT

At the beginning of the Neogene a remarkable faunal turnover occurred within the North American carnivore community. The dominant larger Oligocene carnivores (creodonts, nimravid cats, the amphicyonid *Daphoenus*) became extinct during the late Oligocene and were replaced in the early Miocene by amphicyonine amphicyonids and hemicyonine ursids that entered North America from Eurasia. During a five million-year interval from ~23 to 18 Ma, large amphicyonines appear in late Arikareean and early Hemingfordian faunas of the North American midcontinent. Although most fossils are from western Nebraska and southeastern Wyoming, occurrences of amphicyonines at several sites in the eastern United States (Delaware, Florida) indicate that they rapidly established a broad geographic distribution in North America during the early Miocene.

This report describes and summarizes the North American specimens of the rare immigrant amphicyonine *Ysengrinia*, the first large amphicyonine to enter the New World. *Ysengrinia* exists in North America from ~23 to 19 Ma, becoming extinct at the end of the late Arikareean. A single species of *Ysengrinia* is recognized in North America: *Y. americana* (Wortman, 1901), comb. nov., restricted to the late Arikareean of western Nebraska and southeastern Wyoming. The North American hypodigm includes the only known complete skull of the genus, associated with a mandible and partial postcranial skeleton. Because most Eurasian occurrences of *Ysengrinia* are limited to mandibles or isolated teeth of single individuals, intraspecific variation in teeth and skeleton in these carnivores has been difficult to determine. The more complete North American specimens provide estimates of dental and osteological variation in *Ysengrinia*, and suggest that the North American species is dimorphic. Skeletal remains of early Miocene New World *Ysengrinia* are most often found in riparian and waterhole environments.

INTRODUCTION

Faunal turnover profoundly altered integrated mammalian communities at various times during the Neogene in both North America and Eurasia. These turnover events produced changes in faunal composition throughout the Holarctic region that eventually influenced the southern continents, first Africa in the early Miocene, and later South America in the Plio-Pleistocene. On each occasion, extinction of multiple lineages was followed by the appearance of a new faunal association. Nowhere is this pattern more evident than in the turnover of large carnivorans during the Neogene of North America.

Large carnivorans >200 kg did not exist in the New World at the beginning of the Neogene. The largest carnivores of the North American late Paleogene were an aggregation of diverse, mid-sized (<100 kg in most cases) nimravid cats, creodonts, and amphicyonids. This carnivoran assemblage became extinct during the late Oligocene with the gradual disappearance of Nimravinae, creodonts (Hyaenodontidae), and the daphoenine amphicyonid *Daphoenus*. In the early Miocene a new community of large carnivorans appeared in North America (fig. 1, NALCTE), comprising large amphicyonine beardogs, hemicyonine ursids, and diverse species of the amphicyonid *Daphoenodon*.

The temnocyonine amphicyonids were the only major group of large carnivorans to span the Paleogene-Neogene boundary in North America, apparently unaffected by this North American large carnivore turnover event (NALCTE). Temnocyonines first appeared in the early Arikareean (~29–30 Ma) and diversified into several lineages (Hunt, 1998b) that attained their maximum size (~40–80 kg) in the late Arikareean. The subfamily became extinct at the end of the late Arikareean in North America.

By the mid-Miocene, creodonts were reduced to relict species in Africa, southern Asia, and Europe (Barry, 1980, 1988; Ginsburg, 1980; Morales et al., 1998). Nimravids were represented in the mid- to late Miocene of Eurasia and North America by a single subfamily, the Barbourofelinae (Geraads and Güleç, 1997), of which only a few species (*Barbourofelis fricki*, North America, to ~6 Ma; nimravid, Asian Siwaliks, to ~7.4 Ma; Barry and Flynn, 1989) persisted to near the end of the epoch. The numerous genera and species of late Eocene-Oligocene Nimravi-

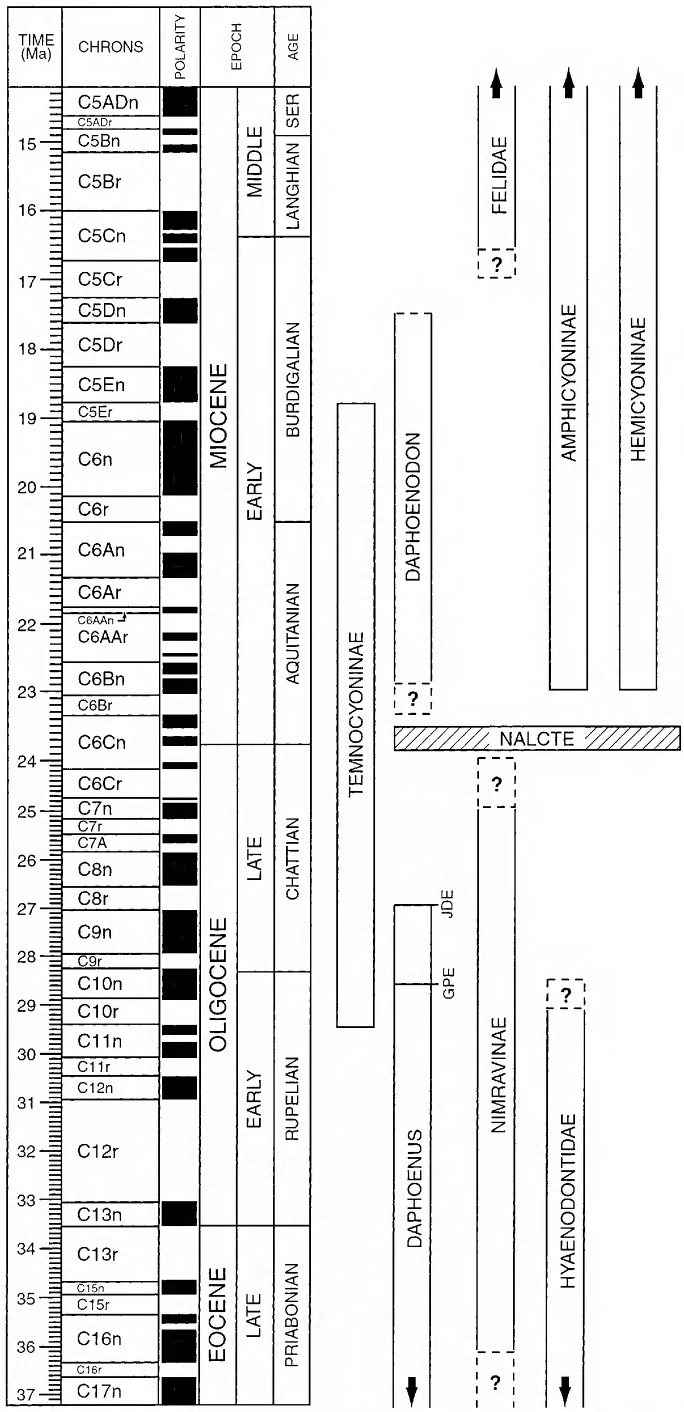


Fig. 1. Temporal ranges of large Oligocene and early Miocene carnivores in North America, demonstrating the faunal turnover event at the Paleogene-Neogene boundary (Global Polarity Time Scale from Berggren et al., 1995). Abbreviations: NALCTE, North American large carnivore turnover event; GPE, last appearance in Great Plains; JDE, last appearance in John Day Formation, Pacific Northwest; Ma, Mega-annum.

nae found in North America and Eurasia were extinct by ~24–25 Ma, prior to the Miocene.

By the end of the early Miocene, amphicyonids and hemicyonines dominated niches for large carnivores on the northern continents (Hunt, 1998a, 1998b; Ginsburg and Morales, 1998). During the mid-Miocene, these were the first Neogene carnivorans to attain sizes >200 kg: among the largest of these arctoids were *Amphicyon ingens* of North America, and the European *Amphicyon giganteus* and hemicyonine *Dinocyon thenardi*. By the mid-Miocene several amphicyonids, including a large species of *Amphicyon*, had entered Africa and rapidly penetrated to the southern limit of the continent (Arrisdrift fauna, Namibia: Hendey, 1978; Morales et al., 1998).

Amphicyonids and hemicyonines continued to dominate the carnivoran fauna of Holarctica into the late Miocene. But within the late Miocene, during the Clarendonian land mammal "age" of North America and the Vallesian of Europe, both groups became extinct. Relict taxa of amphicyonids survived in Africa at Lothagam (Kenya) to at least ~6.5 Ma (Werdelin, 1999), and on the Indian subcontinent in the Siwalik Group to ~7.4 Ma (Barry et al., 1982: 112), but failed to reach South America. After ~9 Ma, late Miocene (Turolian, Hemphillian) faunas on the northern continents lacked amphicyonids and hemicyonines altogether; they were replaced by large ursids (*Agriotherium*, *Indarctos*), felids, and canids—lineages that heralded the eventual rise to prominence of these families in the Plio-Pleistocene.

Ecological roles occupied by amphicyonids and hemicyonines on the northern continents were eventually filled in the Pleistocene/Holocene by ursine bears (Ursidae, *Ursus*, *Thalarctos*, *Arctodus*, *Tremarctos*), the great cats (Felidae, *Panthera*, *Smilodon*, *Dinobastis*), wolves (Canidae, *Canis*), and hyenas (Hyaenidae, *Crocuta*, *Hyaena*, *Parahyaena*, *Pachycrocuta*, *Chasmaporthetes*).

Thus, the early to mid-Miocene interval in North America is identified by a discrete association of large amphicyonids and hemicyonines that intervenes between the late Eocene-Oligocene creodont-nimravid-*Daphoenus* association and the late Miocene to Pleistocene ursid-felid-canid association (Hunt and Tedford, 1993).

This report is one in a series of publications that explores the early Neogene radiation of the Amphicyonidae in the New World. Earlier studies reviewed the Oligocene amphicyonids of North America (Hunt, 1996, 1998b, 2001), the evolution of the family in North America (Hunt, 1998b), and the intercontinental migration of the large amphicyonine *Amphicyon* to the New World in the early Miocene (Hunt, in press). Here I briefly review the early history of amphicyonids in North America (the temnocyonines and endemic daphoenines); describe the faunal turnover event (NALCTE, fig. 1) at the Paleogene-Neogene boundary when creodonts, nimravine cats, *Daphoenus*, and temnocyonines were replaced by immigrant amphicyonines and hemicyonines; and place on record the first of the large immigrant amphicyonines to appear in North America, the Eurasian beardog *Ysengrinia*.

Abbreviations

Anatomical

A	alisphenoid
BO	basioccipital
eam	osseous external auditory meatus
gf	postglenoid foramen
h	hypoglossal (condyloid) foramen
ips	inferior petrosal venous sinus
M	mastoid process
me	mastoid-exoccipital suture
p	petrosal promontorium
pcf	posterior carotid foramen
pg	postglenoid process
plf	posterior lacerate foramen
pp	paroccipital process
T	ectotympanic

Institutional

ACM	Pratt Museum, Amherst College, Massachusetts
AM	Department of Mammalogy, American Museum of Natural History, New York
AMNH	Division of Paleontology, American Museum of Natural History, New York
CM	Division of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh
CNHM	Field Museum of Natural History, Chicago

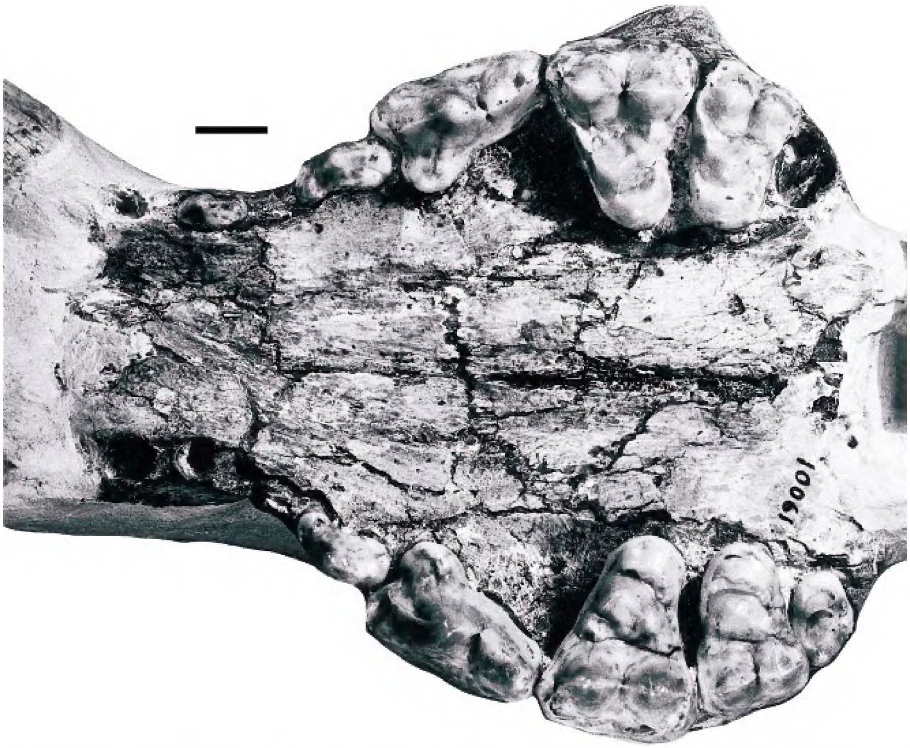


Fig. 2. *Ysengrinia americana* (Wortman, 1901), new combination; holotype palate with left P2–M2, right P3–M3, YPM 10061, upper Arikaree Group, collected in 1875 by H.C. Clifford in northwest Nebraska (see appendix 1). Scale bar, 1 cm.

F:AM	Frick Collection, American Museum of Natural History, New York
FSL	Faculté des Sciences, Université de Lyon, Lyon
MGL	Musée Guimet d'Histoire Naturelle, Lyon
NMB	Naturhistorisches Museum, Basel
PaN	Museo Paleontológico de Valencia, Universidad de Valencia
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UNSM	University of Nebraska State Museum, Lincoln
USNM	Department of Paleobiology, Smithsonian Institution, Washington, D.C.
YPM	Peabody Museum, Yale University, New Haven
ZM	Division of Mammals, University of Nebraska State Museum, Lincoln

EARLY HISTORY OF THE AMPHICYONIDAE IN NORTH AMERICA

The first North American amphicyonids appear in the late Eocene at ~39–40 Ma (Hunt, 1996). The late Eocene to mid-Oligocene (Duchesnean–Chadronian through Whitneyan) species all belong to the endemic North American subfamily Daphoeninae, comprising four genera (*Daphoenus*, *Daphoenictis*, *Brachyrhynchocyon*, *Paradaphoenus*). *Daphoenus* is the oldest New World amphicyonid, appearing in the Duchesnean, and is the most plesiomorphic in dental, cranial, and postcranial features. The small hypercarnivore *Daphoenictis* is first recorded in the later Duchesnean (Hunt, 1996; fig. 2). *Daphoenus*, *Daphoenictis*, and *Brachyrhynchocyon* all occur in the Chadronian, and the latter two genera are not known after that time. *Paradaphoenus* is first certainly known in the Orellan (early Oligocene) and, together with *Daphoenus*, it continued through the Whitneyan into the early Arikareean (late Oligocene; Hunt, 2001). These genera, then, comprise a New World amphicyonid assemblage characteristic of the late

Eocene to late Oligocene interval, all smaller carnivorans of less than 20 kg.

In North America the only significantly larger carnivores that occurred in this fauna were the massive endemic Chadronian creodont *Hemipsalodon* (Mellet, 1969; Gustafson, 1986) and the largest species of North American *Hyaenodon*, *H. megaloides* and *H. horridus* of the Chadronian and Orellan, with skull lengths of 25–40 cm (Mellett, 1977). These creodonts were the only species that approached and, in some cases, exceeded 100 kg. A few early Arikareean nimravid cats were of comparable size, with males possibly approaching 100 kg. However, the small size of most carnivores at this time is in marked contrast to the many large ungulates (brontotheres, rhinoceroses, entelodonts) in the late Eocene-Oligocene of North America.

By the beginning of the Arikareean (~29–30 Ma), the character of the amphicyonid fauna had begun to change. The North American temnocyonine amphicyonids first appear in the earliest Arikareean (Hunt, 1998b), the most primitive species showing a resemblance to *Daphoenus*. The last record of *Daphoenus* (~28.5 Ma in the Great Plains, ~27 Ma in the John Day beds, Oregon) is almost concurrent with the first appearance of temnocyonines at ~29.5 Ma in the John Day Formation, Logan Butte, Oregon (fig. 1).

Temnocyonines diversify and increase in size throughout the Arikareean (fig. 1), but are absent from earliest Hemingfordian faunas and are therefore presumed extinct by ~18.5 Ma. The largest species probably attained ~40–90 kg. They are best represented in the Arikaree Group of the Great Plains and John Day beds of the Pacific Northwest, with rare occurrences from Florida and California.

Temnocyonines are the only group of large carnivorans that bridge the temporal hiatus that occurs between the Paleogene and Neogene large carnivore associations in North America (fig. 1). They span the interval between the last occurrence of endemic *Daphoenus* (~27 Ma) and the first appearance of *Daphoenodon* and immigrant amphicyonines (~23 Ma). The Oligocene-Miocene boundary, placed at ~22.9–23.8 Ma in western Europe (Steininger et al., 1989, 1996, 1997; Shackleton et al., 2000), occurs within the Arikareean NALMA (30 Ma– ~18.8 Ma, MacFadden and Hunt, 1998; Tedford et al., 1996). Therefore, late Arikareean temnocyonines, which are all younger than ~22.9 Ma, are among the oldest Neogene amphicyonids in North America. Temnocyonines (and species of *Daphoenodon*) are the most frequently encountered New World amphicyonids in the earliest Miocene when the subfamily is represented by three lineages (*Temnocyon*, *Mammacyon*, and an undescribed genus).

In Europe, the haplocyonines are related to the Temnocyoninae, and evolved similarly specialized dentitions in parallel at about the same time (Bonis, 1973; Bonis and Guinot, 1987).

Near the Oligocene-Miocene boundary, the beardog *Daphoenodon* appears in North America (fig. 1). Early occurrences are primarily in Florida where a small species, *D. notionastes*, has been identified by fragmentary remains coming from a number of Arikareean fissure fills and karst sinkholes (Frailey, 1979). This species is also known from east Texas, suggesting a restricted Gulf Coastal Plain range (Albright, 1996). *Daphoenodon*, however, is better known from a succession of chronospecies from upper Arikaree and lower Hemingford Group sediments in western Nebraska and southeastern Wyoming (Hunt, 1998b). These fossils are found in fluvial, waterhole, and eolian sediments of a semiarid continental interior. The oldest of the Great Plains species is represented by an undescribed mandible from the type area of the Harrison Formation, estimated at ~22–23 Ma, and hence close to the Oligocene-Miocene boundary. It directly precedes in time a population sample of the holotype species, *D. superbus*, from the waterhole bonebed and carnivore dens at Agate National Monument (Peterson, 1910; Hunt, 1990). The genus is known only from North America, and possibly is derived from the endemic North American Oligocene daphoenine *Daphoenus*.

EARLY NEOGENE AMPHICYONINES

In the early Neogene three European amphicyonine genera appear successively in the New World at ~23 Ma (*Ysengrinia*), ~19.2

Ma (*Cynelos*), and ~18.5–18.8 Ma (*Amphicyon*). These North American first occurrences are interpreted as Eurasian immigrants because of their earlier presence in Europe and their more advanced stage of evolution relative to the earliest Old World species. There are no plausible ancestors for these amphicyonines among North American beardogs. *Cynelos* and *Ysengrinia* have been reported previously from the latest Arikareean of western Nebraska (Hunt, 1972, 1998b), dated at ~19.2 Ma. Recently discovered evidence of *Ysengrinia* in older late Arikareean rocks of western Nebraska, estimated at ~23 Ma, indicates an earlier entry into North America. *Amphicyon* is the last of the three genera to appear, first known from early Hemingfordian sediments in northern Colorado and northwest Nebraska at ~18.5–18.8 Ma (Hunt, in press; MacFadden and Hunt, 1998).

Ysengrinia occurs in both the late and latest Arikareean intervals in North America (~23–18.8 Ma). *Cynelos* first appears in the latest Arikareean (~19.2 Ma), represented by two teeth found in waterhole bonebeds at Agate Fossil Beds National Monument, Sioux County, Nebraska (Hunt, 1972: fig. 6B, D). *Cynelos* and *Amphicyon* are also present in the early Hemingfordian, but are rare, whereas they are the common large amphicyonines of the late Hemingfordian. The robust *Cynelos idoneus* is present in the late Hemingfordian Sheep Creek Formation of western Nebraska where it is accompanied by the even larger *Amphicyon frendens*. These two genera persist as large carnivorans in the early Barstovian. *Cynelos* is not found in the mid-Barstovian and is presumed to be extinct. *Amphicyon* survives into the mid-Barstovian at Horse and Mastodon Quarry, Colorado, but by ~14 Ma is also extinct. *Amphicyon* and *Cynelos* are replaced in the late Barstovian by the amphicyonids *Pseudocyon* and *Ischyrocyon* (Hunt, 1998b), best represented at sites in the Great Plains and California. Both genera are no longer in evidence by the end of the Clarendonian (~9 Ma).

HISTORY OF DISCOVERY OF NORTH AMERICAN *YSENGRINIA*

In North America the first record of *Ysengrinia* is a palate with nearly complete dentition (fig. 2), an upper canine, and a calcaneum of a young adult beardog, discovered in northwest Nebraska in 1875 by H.C. Clifford, at that time in the employ of O.C. Marsh of Yale University (appendix 1). The amphicyonid palate was later designated the holotype of "*Amphicyon*" *americanus* by Jacob Wortman (1901).

Wortman's (1901) published paper reported that the palate was found in the "Loup Fork beds, Niobrara River, Nebraska" and did not mention Clifford or the 1875 date of collection, information recorded only in the YPM catalogue. Casts of the palate which I had previously examined in various museums were poorly executed. In December 2000, I examined the original specimen: its exceptional preservation has prompted this review of the genus in North America, supplementing (and superceding in part) my earlier remarks (Hunt, 1998b). Because all other North American specimens of *Ysengrinia* discovered since 1875 can be attributed to a single species, Wortman's (1901) species-group term serves as the name-bearer for the hypodigm. Hence, the palate (YPM 10061) becomes the holotype of the North American species, *Ysengrinia americana*, comb. nov.

Following Clifford's discovery of the holotype, no new material of *Ysengrinia* came to light in North America until several foot and limb bones were found in early Miocene upper Arikaree rocks of western Nebraska by O.A. Peterson from 1904 to 1908. These were initially attributed to large canids by Peterson (1910). Hunt (1972) later described isolated teeth, an edentulous mandible, and some postcranials (including Peterson's specimens), recognizing them as amphicyonids and referring them to (?)*Ysengrinia* Ginsburg, 1965. Although Peterson (1910) and Hunt (1972) initially attributed these fossils to the Harrison Formation, Hunt (1978, 1985, 1990) later referred the localities to the lower part of the overlying Upper Harrison beds, based on lithostratigraphic revision of the upper Arikaree Group in its type area in Sioux County.

In 1937, collectors from the Frick Laboratory (AMNH) discovered an associated skull, mandible, and postcranials of a large adult *Ysengrinia* in the Upper Harrison beds of southeastern Wyoming (fig. 3), but it re-

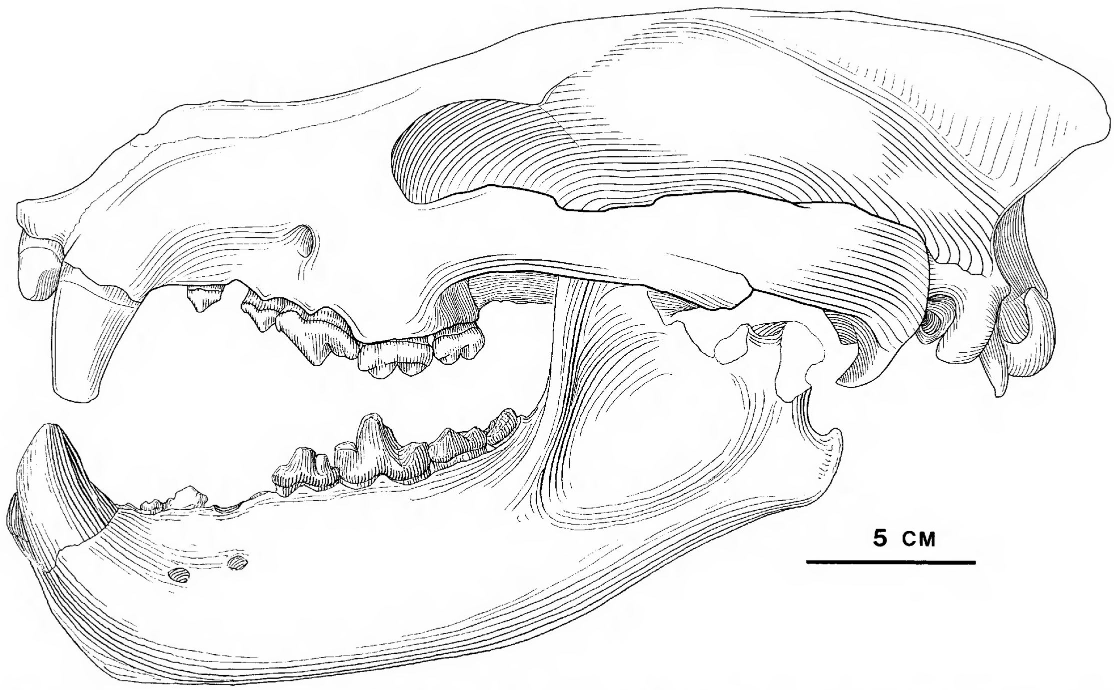


Fig. 3. *Ysengrinia americana*, paratype cranium and associated mandible, F:AM 54147, Upper Harrison beds, 25 Mile District, latest Arikareean, Goshen County, Wyoming.

mained unidentified. This individual (F:AM 54147) demonstrates for the first time an associated upper and lower dentition, the form of the skull, and a damaged but largely intact basicranium, features unknown in Old World *Ysengrinia*. The postcranials were limited to cervical vertebrae and forelimb elements, but nevertheless reveal a short-footed, robust skeleton, similar to the postcrania of *Amphicyon* (Ginsburg, 1961; Hunt, in press). No complete skull is known from the Old World; the Wyoming skull is the first of its kind.

University of Nebraska excavations from 1974 to 1990 at Harper Quarry and other nearby latest Arikareean sites in western Nebraska produced additional remains of *Ysengrinia* (Hunt 1978, 1990). *Ysengrinia* was common in waterhole and riparian environments of this age. In addition to these latest Arikareean fossils, a large collection of isolated teeth, mandibles (most edentulous), and unassociated postcranials were excavated by the University of Nebraska State Museum from the early Hemingfordian Bridgeport Quarries, Morrill County, Nebraska, during 1932–1940. These quarries sampled an early Miocene waterhole environment in which scattered skeletal remains of a variety of mammals were buried. The teeth and bones of a large amphicyonid similar to *Ysengrinia americana* were intermixed with these remains. In a recent summary of amphicyonid diversity in North America (Hunt, 1998b), I allocated this large Bridgeport amphicyonid to *Ysengrinia*. Discovery of the exceptionally preserved palate and dentition of Wortman's holotype of "*Amphicyon*" *americanus* demonstrates that the early Hemingfordian Bridgeport carnivore is better allocated to another taxon (Hunt, in preparation).

GEOGRAPHIC AND GEOLOGIC DISTRIBUTION OF NORTH AMERICAN *YSENGRINIA*

All North American specimens of *Ysengrinia* are from nonmarine sediments of late or latest Arikareean age in western Nebraska and southeastern Wyoming (fig. 4). The earliest North American record of *Ysengrinia* is a mandible with p3–m2 from late Arikareean fluvial sediments at Wildcat Ridge, south of

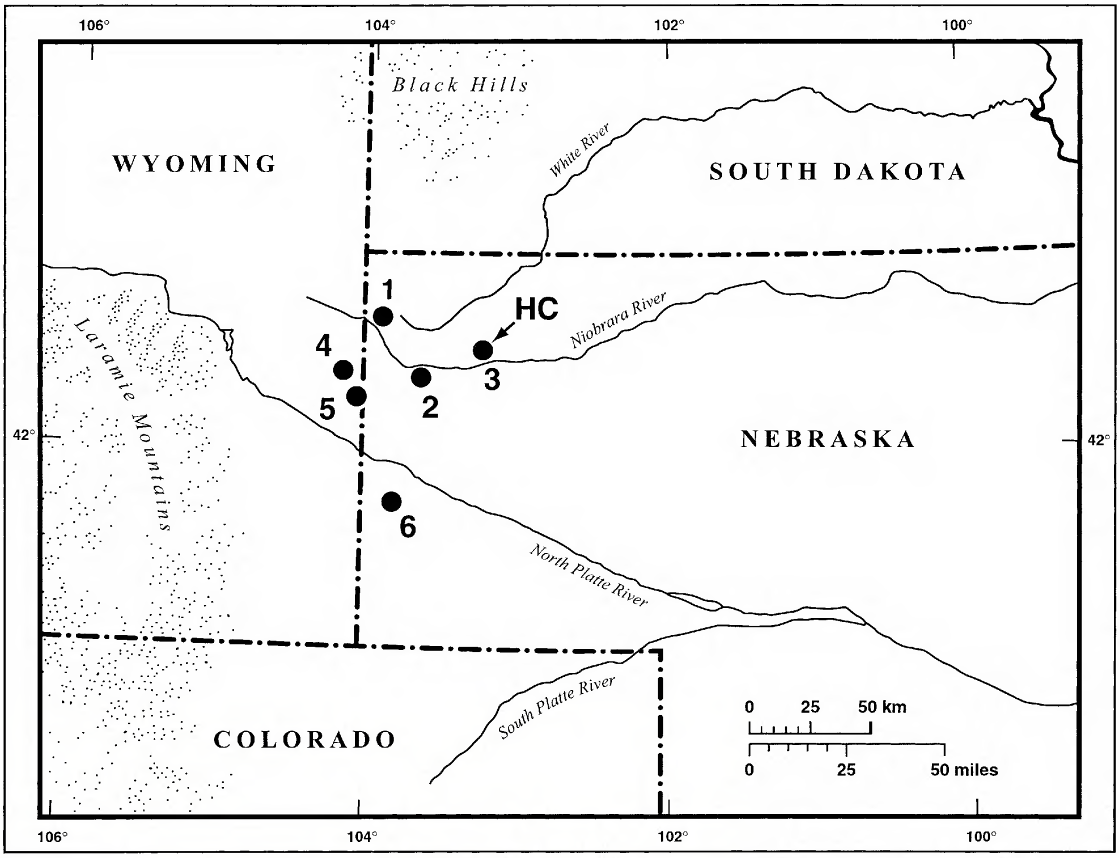


Fig. 4. Geographic distribution of *Ysengrinia* in the North American midcontinent. Localities 1–5, latest Arikareean; locality 6, late Arikareean: 1, Harper Quarry; 2, University Quarry at Agate National Monument and American Museum–Cook Quarry; 3, Morava Ranch Quarry; 4, 25 Mile District of Frick Laboratory, AMNH; 5, Lay Ranch beds (an Upper Harrison paleovalley) at Spoon Butte; 6, UNSM Locality Sf-105; HC, the geographic area where H.C. Clifford collected the holotype (YPM 10061) of *Y. americana*, possibly from Morava Ranch Quarry (appendix 1). All localities are in strata of the upper Arikaree Group.

Gering, Nebraska (Harrison Formation, estimated age, ~23 Ma).

A latest Arikareean sample of *Ysengrinia* includes fossils from the waterhole bonebeds (~19.2 Ma: University Quarry at Agate National Monument, Hunt, 1972, 1990; Harper Quarry, Hunt, 1978; Morava Ranch Quarry, Coombs and Coombs, 1997; AMNH-Cook Quarry, Hunt, 1972) that occur in the basal Upper Harrison beds along the valley of the Niobrara River in Sioux and Box Butte Counties, Nebraska. If Clifford's holotype palate of *Y. americana* was also found at Morava Ranch Quarry, which seems probable, it is of the same age. Seven to ten individuals are known from these waterholes where *Ysengrinia* apparently was an important scavenger-predator.

From higher stratigraphic levels within the Upper Harrison beds of latest Arikareean age, only three occurrences are known—(1) an associated partial postcranial skeleton (USNM 186993) from the Lay Ranch beds (Hunt, 1985) west of Spoon Butte, Goshen County, Wyoming; (2) isolated teeth and postcranials of one or two individuals from the Lay Ranch beds east of Spoon Butte; and (3) the associated skull, mandible, and partial skeleton (F:AM 54147, paratype of *Y. americana*) from Upper Harrison beds, Goshen County, Wyoming, ~15 miles (24 km) northwest of Spoon Butte.

Ysengrinia americana is accompanied by other large carnivorans in the latest Arikareean Upper Harrison fauna of western Nebraska and southeastern Wyoming. *Ysengrinia americana*, *Daphoenodon superbus*, and a temnocyonine are found in the Agate Quarries local fauna (Hunt, 1985, 1990), collected from waterhole deposits and carnivore dens at the base of the Upper Harrison in Sioux County. At higher stratigraphic levels in the Upper Harrison beds of southeastern Wyoming, *Y. americana* and two large undescribed amphicyonid species are associated with faunas age-equivalent to the Niobrara Canyon local fauna (Hunt, 1985, 1990). Also present in the Upper Harrison is the giant mustelid, *Megalictis ferox* (Hunt and Skolnick, 1996), and two species of large temnocyonine amphicyonids representing the terminal members of their respective lineages. Both paleofelids (Nimravidae) and neofelids (Felidae) are absent from these assemblages (Hunt and Joeckel, 1988), and consequently several of these arctoid carnivorans apparently occupied the niches for large cat-like predators.

The Harper Quarry waterhole assemblage (Harper Quarry local fauna: Hunt, 1978, 1985, 1990) produced the most numerous postcranial remains of *Y. americana*—although at least four individuals are represented, there were no articulated elements. No crania or mandibles have been found, only isolated teeth. Scavenging at the waterhole is everywhere evident, suggesting that skulls were fragmented and scattered.

Ysengrinia americana is present but rare in the waterhole bonebeds in the vicinity of Agate Fossil Beds National Monument (Hunt, 1972). A robust metacarpal was found in the waterhole bonebed at University Hill in 1904, but no remains have come from the quarries at Carnegie Hill and the nearby carnivore den site (Hunt et al., 1983; Hunt, 1990). At the American Museum–Cook Quarry waterhole, located a few kilometers north of the Agate waterhole bonebed, *Ysengrinia* is represented by a calcaneum and M1.

Fragmentary remains of *Y. americana* at Morava Ranch Quarry include an edentulous mandible (F:AM 25423), isolated M1, a partial innominate, distal humerus, ectocuneiform, and a few phalanges (Hunt, 1972: figs. 8, 9, 10A, 11). The depositional environment of Morava Ranch Quarry fossils has been described by Coombs and Coombs (1997) as a waterhole in a fluvial setting. The diagnostic M1 of *Ysengrinia americana* is known from Morava Ranch Quarry and from American Museum–Cook Quarry (Hunt, 1972: fig. 10A, B). These molars are nearly identical to the M1 of the holotype and paratype. Despite the lack of teeth in the Morava Ranch mandible, its deep-jawed, robust form, the size and spacing of the alveoli, and the placement of the mental foramina demonstrate a correspondence to the mandible of the *Y. americana* paratype.

Although *Ysengrinia* is uncommon in Upper Harrison sediments (Lay Ranch beds, Hunt, 1985) filling the Lay Ranch paleovalley at Spoon Butte, the few scattered occurrences include an associated partial hindlimb that establishes the proportions of femur to tibia, and provides insight into the functional anatomy of the hindfoot. This partial skeleton of a large individual, probably male, was discovered and excavated in 1972 west of Spoon Butte by R.J. Emry and M.F. Skinner for the Smithsonian Institution. In the same paleovalley east of the butte, a partial mandible of a much smaller individual was found by UNSM in 1983, suggesting that sexual dimorphism was an attribute of *Y. americana* populations. Evidence of dimorphism occurs not only in the Lay Ranch beds in southeastern Wyoming but also at Harper Quarry in northwest Nebraska where marked size differences are evident in some postcranial bones.

Finally, a large "canid" humerus (CM 2400) was reported by Peterson (1910: fig. 56) from a quarry 8–10 miles east of the Agate Quarries. This humerus was later refigured and described by Hunt (1972) and attributed to (?)*Ysengrinia*. Peterson's quarry has never been relocated, and no other fossils from this quarry were identified in the collections of the Carnegie Museum (Pittsburgh), despite Peterson's (1910: 262) statement that the "quarry . . . contains a similar fauna to that of the Agate Spring Fossil Quarries". The anatomy of the distal humerus indicates referral to *Y. americana*.

SYSTEMATICS

ORDER CARNIVORA BOWDICH, 1821

DIVISION ARCTOIDEA FLOWER, 1869

FAMILY AMPHICYONIDAE TROUESSART, 1885

Ysengrinia Ginsburg, 1965

TYPE SPECIES: *Ysengrinia gerandiana* (Viret).

INCLUDED SPECIES: *Ysengrinia americana* (Wortman), comb. nov., *Y. tolosana* (Noulet), *Y. depereti* (Mayet), *Y. valentiana* Belinchon and Morales, ?*Y. ginsburgi* Morales, Pickford, Soria, and Fraile.

KNOWN DISTRIBUTION: Early Miocene (late to latest Arikareean) of southeastern Wyoming and western Nebraska; late Oligocene-early Miocene of France (MP 30, MN1–3); early Miocene of Germany; late early Miocene of Spain (MN4); ?late early Miocene of southwest Africa (MN4).

DIAGNOSIS: Mid-sized to large (~40–150 kg) deep-jawed amphicyonines (anteriorly deep mandibles do not occur in daphoenines) in which the posterior molars (M2–3, m2–3) are not enlarged to the degree observed in mid-Miocene *Amphicyon* (table 1).

Anterior premolars (p1–3, P1–3) are low, reduced, differing from North American temnocyonines and *Daphoenodon* in which the anterior premolars are well-developed; p4 in *Ysengrinia* is not reduced, has a tall principal cusp equal in height to the m1 paraconid, and a well-developed posterior accessory cusp above an expanded cingulum shelf; p4 has a rounded posterior margin (*Daphoenodon* has a squared posterior margin) and, as noted by Bonis (1973), a nearly rectilinear mesial face. The m1 is robust, wide, carnassiform, with massive trigonid and prominent low talonid (m1 in contemporary *Cynelos* is much smaller and less robust); a slightly swollen m1 metaconid is present and is situated at the same height as the paraconid—it becomes somewhat reduced in *Y. depereti* but is present in *Amphicyon* and *Daphoenodon*; the m1 talonid has a prominent labially placed, ridgelike hypoconid, bordered internally by a low shelf lacking a defined entoconid cusp.

The m2 is considered diagnostic and occurs in a mandible of *Y. gerandiana* (MGL St.-G. 2848), the type species of *Ysengrinia*, figured by Viret (1929: pl. VII, fig. 1, text-fig. 17). The m2 is elliptical in occlusal view, robust, but not enlarged relative to m1; the m2 trigonid is large and moderately elevated relative to the short, low talonid (the rectangular m2 of *Amphicyon*, *Cynelos*, and most species of *Daphoenodon* differs in having a more elongated, wider talonid). The principal trigonid cusp is a massive, slightly labially placed protoconid. A thin crest runs anterolingually from the protoconid to form an arcuate rim at the front of the tooth that terminates at the location of a very reduced or absent paraconid. The swollen metaconid is much smaller than the taller protoconid and is separated from it by a shallow cleft or valley. The posteriorly tapering m2 talonid appears to be much reduced relative to the robust trigonid; the m2 talonid displays a prominent, ridged, labially placed hypoconid. There is no entoconid. The labial faces of the m2 hypoconid and protoconid are smoothly rounded whereas the inner faces of these cusps are lingually inclined and flat. The dental formula is 3-1-4-3/3-1-4-3 (temnocyonine amphicyonids and canids have lost M3).

M2–3/m2–3 are not enlarged, but remain subordinate in size to M1/m1. Thus, *Ysengrinia* differs from both Old and New World mid-Miocene *Amphicyon* species (Old World *A. giganteus*, *A. major*, New World *A. frendens*, *A. ingens*) in lacking greatly enlarged posterior molars. *Ysengrinia* differs from contemporary species of *Cynelos* in being much larger.

EUROPEAN SPECIES OF *YSENGRINIA*: *Ysengrinia* was created by Ginsburg (1965) for two mandibles and a tentatively referred rostrum from St.-Gérand-le-Puy (Allier, France) that had been originally referred by Viret (1929) to *Pseudocyon gerandianus*. Viret did not present a compelling rationale for assigning the three specimens to *Pseudocyon*. Ginsburg pointed out that the rostrum could not represent *Pseudocyon*, since upper molars had been found in association with a typical lower dentition of *Pseudocyon* (Kuss, 1965: fig. 79) at Ponsan-Soubiran, France, and these molars were different from those in Viret's rostrum. Therefore, Ginsburg (1965) created a new genus, *Ysengrinia*, for the mandibles and rostrum from St.-Gerand, and the species thus became *Ysengrinia gerandiana* (Viret).

Ginsburg (1966) next placed two additional species in *Ysengrinia*: "*Amphicyon*" *tolosanus* Noulet from the Aquitanian of Paulhiac, and "*Pseudocyon*" *depereti* Mayet from the early Burdigalian of Chilleurs-aux-Bois. These two species were previously referred to *Arctamphicyon* by Kuss (1965), but this assignment was sensibly questioned by Bonis (1973), who noted that because the holotype of *Arctamphicyon* is an isolated M2 from the Siwaliks, and the types of *tolosanus* and *depereti* are mandibles without associated upper dentitions, comparison was not possible. Referral of these species to *Arctamphicyon* is without merit. Nor can *tolosana*, *depereti*, or *gerandiana* be placed in *Pseudocyon* as this genus is presently defined.[2]

In his monograph on Aquitanian mammals of the Agenais district, France, Bonis (1973: 97–100) reviewed *Ysengrinia tolosana*. He included in it Aquitanian fossils from Le Cammas, France (the holotype mandible of Noulet); from Paulhiac, France (the lower teeth of a single individual except for a referred canine); and a mandible from Flörsheim, Germany. These fossils established the characteristics of the lower dentition. Bonis (1973: 99) suggested that Viret's mandible (with m2, MGL St.-G. 2848) of *Y. gerandiana* might be included in *Y. tolosana*, based on the similar size and form of m2 in the two species. However, Ginsburg (1999), Morales et al. (1998), and Ginsburg et al. (1991) continued to employ *Y. gerandiana* as a species distinct from *Y. tolosana*. Ginsburg (1999) recognized *Y. tolosana* in European mammal zones MP30–MN1, *Y. gerandiana* in MN2, *Y. depereti* in MN3, and the recently discovered *Y. valentiana* from Spain (Belinchon and Morales, 1989) in MN4 (table 1).

Neither Viret (1929) nor Ginsburg (1965) selected a type specimen from the two mandibles and the rostrum comprising Viret's hypodigm of *Y. gerandiana*. Although Kuss (1965: 141f.) placed this hypodigm in *Pseudocyonopsis* as a subspecies (*P. landesquei gerandianus*), a generic attribution later refuted by Bonis (1973), he did select from Viret's hypodigm the mandibular fragment with p2–m1 (FSL 213828: Viret, 1929: pl. VII, fig. 3) as the holotype of *gerandiana* (appendix 2).

Only a few fossils attributed to *Ysengrinia* have been reported from the Aquitanian of Germany. The mandible from Flörsheim referred to *Y. tolosana* by Bonis (1973) is similar to the Paulhiac mandible, and displays a p4 resembling that of the North American paratype of *Ysengrinia americana*. A pair of mandibles from Ulm-Westtangente, first illustrated by Heizmann (1992; also Heizmann et al., 1996), are similar to both North American and European mandibles of *Ysengrinia*. These mandibles were recently placed in a new genus, *Crassidia*, by Heizmann and Kordikova (2000), who also placed *Crassidia* in a new tribe, Ysengriniini, together with *Ysengrinia* and *Amphicyonopsis*.

The mandibles of *Crassidia* are associated with only a few upper teeth: P3–4 and an M1 fragment. However, Heizmann and Kordikova also decided that the holotype of *Amphicyon intermedius* H. von Meyer, 1849, an isolated M1 from the Aquitanian Süßwasserkalk near Ulm, Germany, probably belongs to the same species as the mandibles. For this material they established the species *Crassidia intermedia*. Meyer's M1 is similar in size and form to M1 of *Y. americana* (Hunt, 1972: fig. 10A), but differs in lacking the thickened lingual cingulum of the North American species and its distinctive placement posterolingual to the protocone. No complete upper molars are unambiguously associated with lower teeth of *Ysengrinia* in Europe.

In addition to *Ysengrinia*, there were other large beardogs in the Aquitanian of western Europe. Most of these fossils are from France. In the Agenais district, Bonis (1973)

[2] *Pseudocyon sansaniensis* is based on a mandible from Sansan, an apparent female, and on a referred male mandible from Ponsan-Soubiran (Kuss, 1965: fig. 79). These *Pseudocyon* mandibles display an m2 trigonid crowded to the front of the tooth, and a long m2 talonid with a relatively flat occlusal surface. The m2 hypoconid is a low cusp placed close to the labial margin of the tooth. Moreover, the principal cusp of p4 is low, well below the height of the m1 paraconid, whereas in *Ysengrinia* it is a tall cusp approximating the m1 paraconid in height. In *Ysengrinia* the m2 trigonid occupies the entire anterior half of the tooth, the cusps are not crowded to the front of the tooth, and the short talonid has a broad, labial hypoconid occupying more of the talonid surface than in *Pseudocyon*. The m2 form and reduced p4 distinguish *Pseudocyon* from *Ysengrinia*. Although *Pseudocyon* eventually entered North America at ~15.5 Ma (Hunt, 1998b), it does not occur in Arikareean or Hemingfordian faunas of the New World.

TABLE 1
Dental Measurements (in mm) of North American and European Species of *Ysengrinia*

	p2	p3	p4	m1	m2	m3	c-m2	p1-4
Ysengrinia americana								
F:AM 54147	8.3 × 4.0	(13.4)[a]	20.4 × 9.6	28.8 × 14.4	17.7 × 13.1	12.3 × 10.7	111.5	60.7
F:AM 25423	(13.5)	(15.9)	(19.3 × 8.9)	(29.7)	(18.0)	—	~119	~63
UNSM 44673	—	—	—	—	18.8 × 14.5	—	—	—
UNSM 26584	(5.8 × 3.8)	12.1 × 7.4	16.6 × 10.1	27.9 × 14.9	16.7 × 12.3	(8.0 × 6.4)	118.0	69.4
UNSM 7131-83	(8.2)	(12.2)	17.9 × 9.0	—	—	—	—	55.7
Ysengrinia tolosana								
Mus. Toulouse[b]	—	—	16.5 × 9.5	~27 × 13.9	~16 × 13.5[c]	—	—	—
Mus. Darmstadt	(8 × 5)	12 × 6	19 × 9	27 × 14	16 × 12.5	(9 × 6.5)[c]	—	—
NMB Pa 951	—	13.3 × 6.6	18.2 × 9.0	29.0 × 14.1	17.4 × 12.7	—	~62.8	—
NMB Pa 954, 952, 953	—	—	—	29.4 × 14.7	17.7 × 13.7	11.9 × 9.8[c]	—	—
Ysengrinia gerandiana								
MGL St. G. 2848	—	—	—	(25.5)	16.5 × 12.5[d]	—	—	—
FSL 213828[b]	10.8 × 5.9	11.1 × 6.2	15.3 × 8.1	24.3 × 12.1	—	—	—	—
Ysengrinia depereti								
Mus. Orléans 785[b]	(9.6)	(10.3)	(15.6)	30.5 × 14.9	18.3 × 15.1	(11.5)	—	54.1
Ysengrinia valentiana								
PaN 359[b]	—	—	—	—	13.7 × 9.9	—	—	—

	P2	P3	P4	M1	M2	M3	C-M2	P1-4
Ysengrinia americana								
F:AM 54147	10.8 × 5.1	14.7 × 7.2	27.6 × 16.4	21.2 × 28.0	14.5 × 23.2	—	100.6	70.2
YPM 10061[b]								
Left	10.5 × 5.3	14.8 × 7.4	26.9 × 16.8	21.6 × 27.2	16.1 × 23.8	—	~103	67.1
Right	—	15.0 × 7.7	26.9 × 16.5	22.5 × 27.9	15.6 × 23.6	9.3 × 13.4	~103	68.7
F:AM 25420	—	—	—	21.2 × 27.4	—	—	—	—
AMNH 81049	—	—	—	19.4 × 24.0	—	—	—	—
UNSM 44674	—	—	—	—	14.0 × 22.9	—	—	—
Ysengrinia valentiana								
PaN 319	—	—	—	17.5 × 22.0	—	—	—	—

[a] ( ) indicates alveolar measurement.
[b] Holotype.
[c] Kuss, 1965: 85.
[d] Viret, 1929: 121.

recognized a true *Amphicyon* at Laugnac (MN 2b, ~35 km south of Paulhiac), currently designated as *Amphicyon laugnacensis* (Ginsburg, 1989: 104; 1999: 116), and also a large anteriorly deep mandible from Garrouch (MN1), the holotype of *Amphicyon astrei* (Kuss, 1962; Ginsburg, 1999: 144). Fossils of large Aquitanian beardogs are also known from the Allier basin, France, northeast of the Agenais. Viret (1929) described remains of a large deep-jawed amphicyonine from Langy, which he assigned to *Amphicyon crassidens*. Bonis (1973) noted a number of features of the lower dentition that differed from the large amphicyonines of the Agenais. My examination of the holotype m1, a maxilla, and a cast of a mandible from Viret's hypodigm (1929: pl. 3) in Lyon, indicates that these fossils are not referrable to *Ysengrinia*. Recently, Heizmann and Kordikova (2000) placed Viret's specimens of *A. crassidens* in *Crassidia*.

AFRICAN AND ASIAN SPECIES OF *YSENGRINIA*: Two maxillae (one edentulous) and a man-

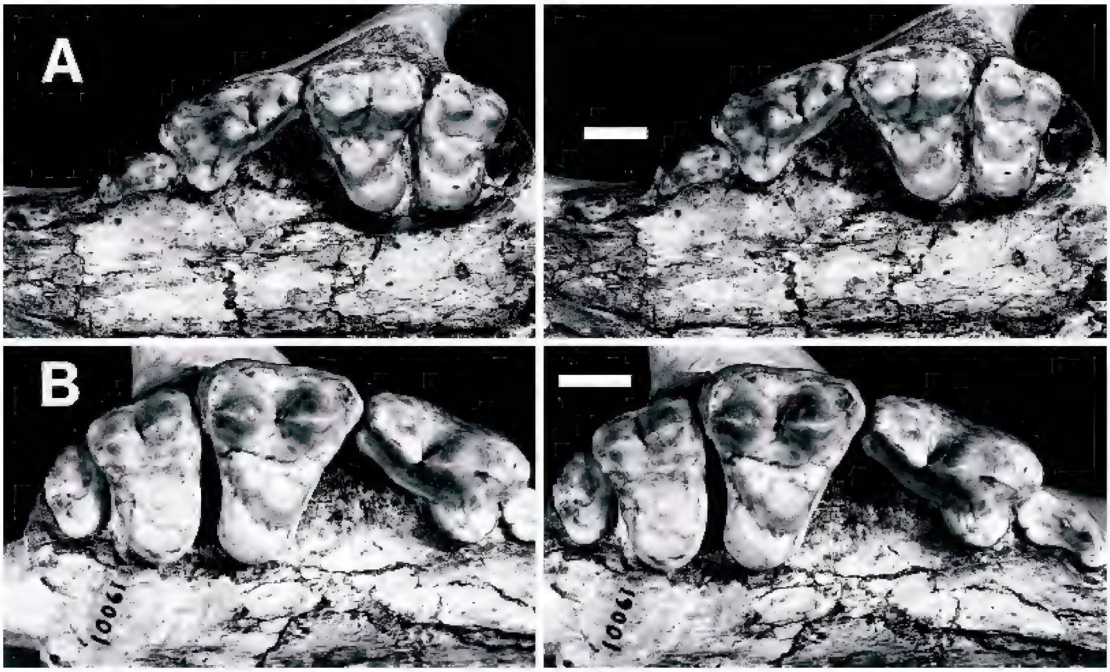


Fig. 5. Holotype dentition of *Ysengrinia americana* (Wortman, 1901), YPM 10061, upper Arikaree Group, northwest Nebraska: **A,** left P2–M2, M3 alveoli; **B,** right P3–M3. Stereophotographs. Scale bars, 1 cm.

dible from the Arrisdrift fauna, Namibia (MN4a, early Miocene), were recently referred to *Ysengrinia ginsburgi* by Morales et al. (1998). If correctly assigned, this is the first and only record of the genus in Africa. Heizmann and Kordikova (2000), however, questioned referral of the holotype mandible to *Ysengrinia* based on features of p4–m2 that differ from most species of the genus.

There are two Asian records of *Ysengrinia*: a maxilla with P4–M2, from the upper part of the Askazansor Formation, Betpakdala, Kazakhstan (early Miocene, MN1–2, Bonis et al., 1997), and an isolated M1 from the Korematsu Formation (~15.6–16.3 Ma), southwestern Japan (Kohno, 1997). The Japanese molar, as noted by Kohno, is quite young to belong to the genus, which previously was not recorded in rocks younger than ~17 Ma. The form of the molar differs from M1 of *Y. americana*, but is extremely similar to M1 of Hemingfordian *Cynelos* (e.g., *Cynelos idoneus*, holotype maxilla, AMNH 18912), whose age better corresponds to the age of the Korematsu Formation. The P4–M2 in the maxilla from Kazakhstan differ proportionately from these teeth in *Y. americana*: the P4 is smaller, M1 larger, and M2 much smaller and narrower than these teeth in North American *Ysengrinia*, and they do not seem to correspond to expected upper dentitions of *Y. tolosana* and *Y. gerandiana* from the equivalent interval (MN1–2) in Europe. Because the upper dentiton of European *Ysengrinia* is not certainly known, more complete material will be required to confirm the presence of the genus in Asia.

Ysengrinia americana (Wortman, 1901), new combination

Figures 2, 3, 5–7, 9–22, 24A, table 1

HOLOTYPE: YPM 10061, palate with right P3–4, M1–3, alveoli for P1–2; left C, P2–4, M1–2, alveoli for P1 and M3 (figs. 2, 5). The Yale catalogue also records a calcaneum with the palate, but it was not with the holotype in the Yale collection, and Wortman (1901) does not mention a calcaneum in his initial description.

HOLOTYPE LOCALITY: From the Yale Peabody Museum Catalogue of Mammalia, Nos.

10001 to 14975: ''YPM 10061, accession no. 704, H.C. Clifford, 1875, palate and teeth, calcaneum''. Probably found by Clifford in upper Arikaree rocks of the Niobrara River valley, northwestern Nebraska, near the Sidney–Red Cloud Agency trail in March 1875. The holotype was apparently collected from an 1875 excavation that was reopened in 1940 by the Frick Laboratory as the Morava Ranch Quarry and was further explored in 1975 by M.C. Coombs (appendix 1).

HOLOTYPE HORIZON: Based on preservation of the teeth and palate, and on information from the Yale Peabody Museum archives, the stratigraphic units from which Clifford could have obtained the holotype are the early Miocene Harrison Formation and Upper Harrison beds of the upper Arikaree Group. If the holotype is in fact from Morava Ranch Quarry, it was collected in the basal Upper Harrison beds.

PARATYPE: F:AM 54147, a complete skull with right I3, C, P1–M2, left damaged I2–3, C, damaged P1–3, intact P4–M2; M3 presumably present, but lost from skull (figs. 3, 6). The skull is associated with a right mandible with worn canine, damaged p1–2, alveoli for p3, and intact p4–m3 (figs. 3, 7). Associated postcranials: axis, third to fifth cervical vertebrae, right humerus, proximal left and right ulnae, distal left radius, left scapholunar, a proximal phalanx (pathologic), right metacarpal 1, left metacarpal 5, and a distal metapodial.

PARATYPE LOCALITY: 25-Mile District of the Frick Laboratory (AMNH), Goshen County, Wyoming, collected by C.H. Falkenbach in 1937 from the ''Middle Brown Sand''.

PARATYPE HORIZON: Detailed stratigraphic information identifying the collecting locality was not recorded in 1937; however, the ''25-Mile District'' was Falkenbach's field term for a collecting area 18 miles south and 7 miles east of the town of Lusk, Goshen County, Wyoming. Exposures that he named ''Middle Brown Sand'' in this area are referred to the Upper Harrison beds of Peterson (1907, 1909; Hunt, 1990). The Upper Harrison beds are of latest Arikareean age.

REFERRED SPECIMENS: From the Upper Harrison beds: Primarily from Harper Quarry, Sioux County, Nebraska, but also from Morava Ranch Quarry, Box Butte County, Nebraska; American Museum–Cook Quarry and University Quarry, Sioux County, Nebraska; and some specimens from the Lay Ranch beds, an Upper Harrison paleovalley fill extending from Goshen County, Wyoming, eastward into Sioux County, Nebraska. From the Harrison Formation: UNSM Locality Sf-105, Wildcat Ridge, Scottsbluff County, Nebraska (fig. 4).

HARPER QUARRY: *Dental:* all isolated teeth—M2, l. (UNSM 44674); I3, l. (UNSM 44687); upper C, r. (UNSM 44670); lower C, r. (UNSM 44672); m1 talonid, r. (UNSM 44671); m2, r. (UNSM 44673); m3, l. (UNSM 44676); *Postcranial:* innominate, partial, l. (UNSM 44626); innominate, partial, r. (UNSM 44627); baculum (UNSM 44629); femur, r. (UNSM 44624); femur, proximal, r. (UNSM 44625); femur, l. (UNSM 44690); tibiae, l. (UNSM 44620, 44622); tibiae, r. (UNSM 44621, 44623); calcaneum, l. (UNSM 44692); calcanea, r. (UNSM 44631, 44632); astragalus, l. (UNSM 44630); metatarsal 1, r. (UNSM 44640); metatarsal 1, proximal, l. (UNSM 44641); metatarsal 2, l. (UNSM 44637, 44639); metatarsal 3, r. (UNSM 44636); metatarsal 4, l. (UNSM 44635); metatarsal 4, r. (UNSM 44638); metatarsal 5, r. (UNSM 44633, 44634); scapula, partial, l. (UNSM 44607, 44608); humerus, l. (UNSM 44606); ulnae, r. (UNSM 44603–44605); radii, l. (UNSM 44600, 44601); radius, r. (UNSM 44691); juvenile radius, diaphysis, r. (UNSM 44602); scapholunars, r. (UNSM 44609, 44693); scapholunar, l. (UNSM 44610); unciform, r. (UNSM 44666); metacarpal 2, l. (UNSM 44616); metacarpal 2, r., without distal end (UNSM 44619); metacarpal 4, r. (UNSM 44617); metacarpal 4, l., without distal end (UNSM 44618); metacarpal 5, r. (UNSM 44611, 44614, 44615); metacarpal 5, r., proximal (UNSM 44613); metacarpal 5, l. (UNSM 44612); proximal phalanges (UNSM 44656–44659, 44665); median phalanges (UNSM 44660–44664, 44678); atlas vertebrae (UNSM 44644, 44645); cervical vertebra (UNSM 44642); thoracic vertebra (UNSM 44643); lumbar vertebrae (UNSM 44646–44655, 44668); caudal vertebra, partial (UNSM 44667); sacrum (UNSM 44628).

NIOBRARA CANYON: *Dental*: partial

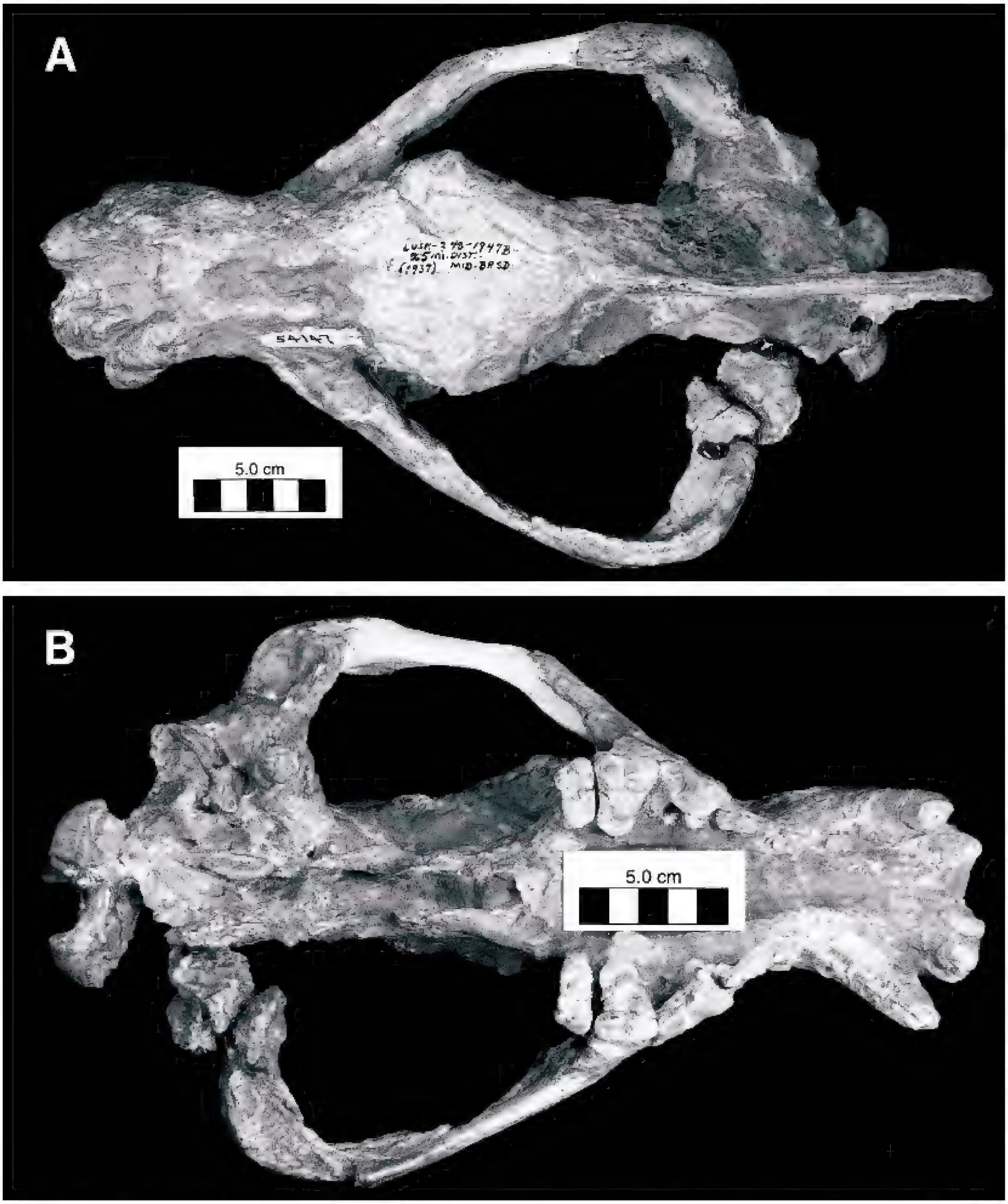


Fig. 6. *Ysengrinia americana*, paratype cranium, F:AM 54147, Upper Harrison beds, 25 Mile District, latest Arikareean of Goshen County, Wyoming. **A,** dorsal view; **B,** ventral view.

maxilla with M1, broken P4, l. (F:AM 54149), from volcaniclastic loess lithofacies, type area, Upper Harrison beds, Sioux County, Nebraska.

MORAVA RANCH QUARRY: *Dental:* isolated M1, l. (F:AM 25420); mandible, edentulous, r. (F:AM 25423); *Postcranial*: innominate, r. (ACM 9761); humerus, distal,

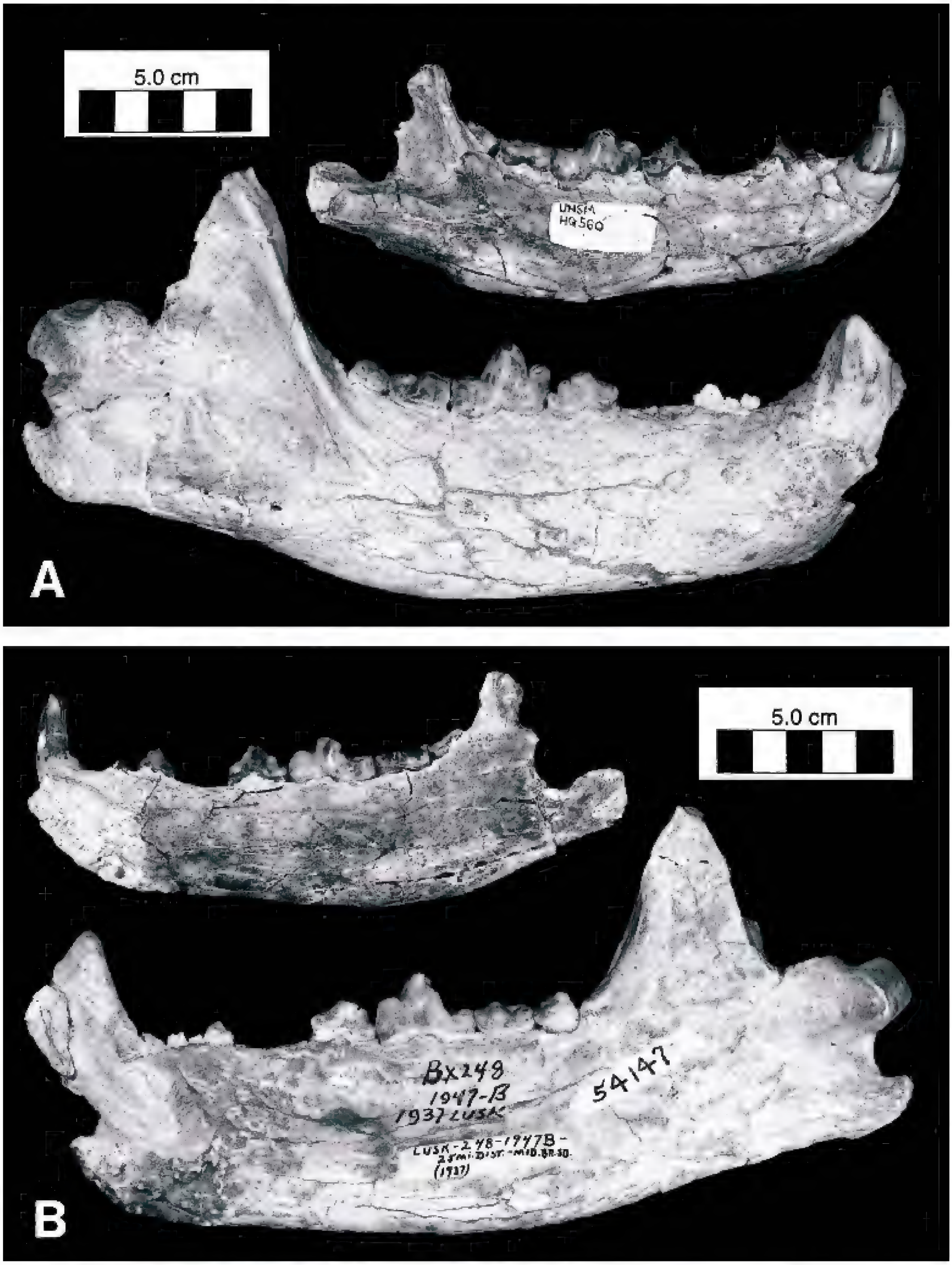


Fig. 7. Mandibles of *Daphoenodon superbus* (UNSM 44688, Harper Quarry) and *Ysengrinia americana* (paratype, F:AM 54147). **A,** lateral view; **B,** medial view.

l. (F:AM 25421); ectocuneiform, r. (ACM 9390); proximal phalanges (F:AM 25433, ACM 9392, and F:AM field no. Har. 211-80); median phalanx (F:AM field no. Har. 211-80).

AMERICAN MUSEUM–COOK QUARRY: *Dental*: isolated M1, l. (AMNH 81049); *Postcranial*: calcaneum, r. (CM 2211).

UNIVERSITY QUARRY (Agate Fossil Beds National Monument): *Postcranial*: metacarpal 5, r. (CM 1897).

LAY RANCH BEDS: West of Spoon Butte, Goshen County, Wyoming: (1) an associated partial skeleton and isolated canine of a single individual (USNM 186993). *Dental:* upper C, r.; *Postcranial*: right and left scapulae, the left femur, tibia, and astragalus, a navicular and pisiform; (2) an isolated proximal phalanx (UNSM 6030-79).

East of Spoon Butte, Sioux County, Nebraska: (1) isolated lingual half of M1 and a metatarsal 2, l. (both UNSM 6109–79); (2) partial right mandible with p4 and alveoli of the canine and p1–3 (UNSM 7131-83).

UNSM LOCALITY Sf-105: *Dental*: (1) mandible, r. with p3–m2 (UNSM 26584).

KNOWN DISTRIBUTION: Late to latest Arikareean of Sioux, Box Butte, and Scottsbluff counties, Nebraska, and Goshen County, Wyoming (fig. 4). Harper Quarry, University Quarry, and the American Museum–Cook Quarry are excavated in waterhole bonebeds that filled with tuff, fine sand, silt, and lime mud (Hunt, 1978, 1990). Morava Ranch Quarry occurs in a fine-grained fluvial channel fill (Coombs and Coombs, 1997). Fossils from these quarries comprise an older Upper Harrison fauna from the base of the unit. Fossils from the Lay Ranch beds near Spoon Butte are slightly younger and come from fine-grained fluvial sediments filling a broad Arikaree paleovalley of Upper Harrison age (Hunt, 1985, 1990). The locality that produced the paratype skull, mandible, and skeleton can only be approximately located; however, matrix on the fossils indicates that they came from a volcaniclastic loess lithofacies of the Upper Harrison beds, and explains the relative degree of completeness of this skeleton (see Hunt, 1990, for descriptions of Upper Harrison lithofacies). The mandible from UNSM locality Sf-105 was found in a fluvial channel fill of a major drainage in the company of numerous other late Arikareean mammals.

DIAGNOSIS: Upper molars particularly diagnostic—M1 with occlusal outline of isosceles triangle, paracone taller than metacone, protocone a low V-shaped platform with lingually directed apex, arms of the V continue as thin enamel ridges to the bases of paracone and metacone; there is no strong development of a metaconule as occurs in *Amphicyon*; a thickened posterolingual cingulum is particularly characteristic—there is no thickening of the anterior cingulum which is not enlarged and merges smoothly with the expanded posterolingual cingulum; a shallow basin occurs between the posteromedial base of the protocone and the enlarged posterolingual cingulum; M2 noticeably smaller than M1; M2 metacone slightly to strongly reduced relative to paracone; metaconule not enlarged; well-developed lingual cingulum surrounding protocone; M3 much smaller than M2, apparently undergoing reduction (in contrast to *Amphicyon* and *Cynelos*); P4 robust with slightly reduced anterolingually directed protocone; paracone with sharp enamel ridge descending anterior face and fusing with cingulum; P4 parastylar cusp absent (present in *Amphicyon*) but short length of cingulum enlarged immediately *labial* to terminus of descending enamel ridge, creating a pseudoparastyle; anterior premolars somewhat reduced; P3 narrow, its length extended by developed anterior and posterior cingula; vertical crease in the enamel occurs at posterolingual corner of P3; snout short and constricted at level of P2 (width at P2, ~50 mm, width at M1, ~92–98 mm in holotype and paratype); P1–2/p1–2 small; anterior mandible deep below p1–3; prominent p4 with posterior accessory cusp but without anterior accessory cusp; m1 robust with tall trigonid, prominent metaconid, talonid dominated by tall, ridgelike, labially placed hypoconid and no entoconid; m2 not enlarged relative to m1 (m2 description as for the genus); m3 a robust, broad, flat enamel platform. Upper canine slightly elongate, with sharp posterior and anterolingual enamel ridges.

Distinguished from *Y. depereti* by smaller average size of m1–m2 (fig. 8, table 1), and by m2 form; from *Y. tolosana* by the form

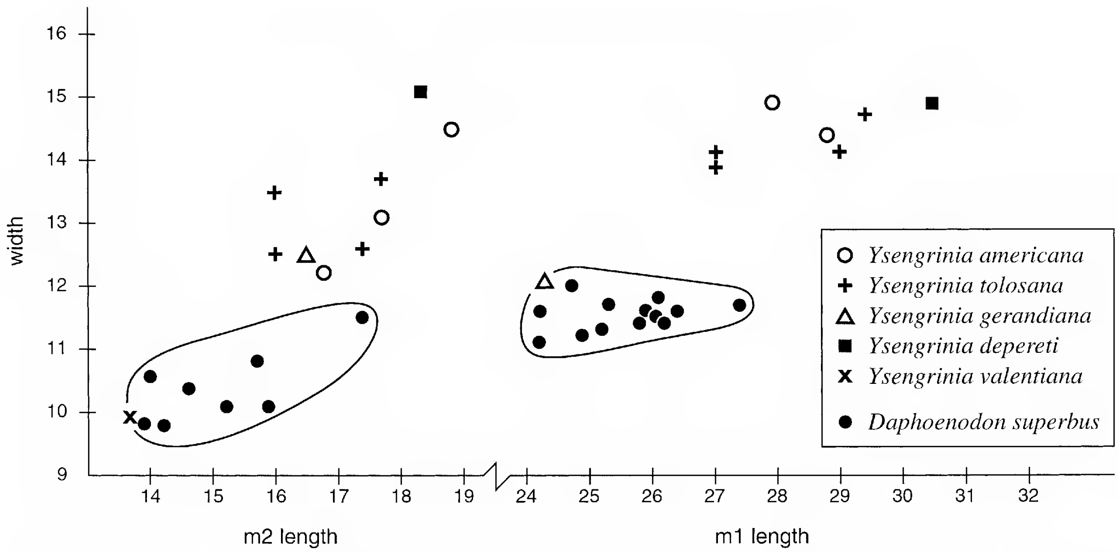


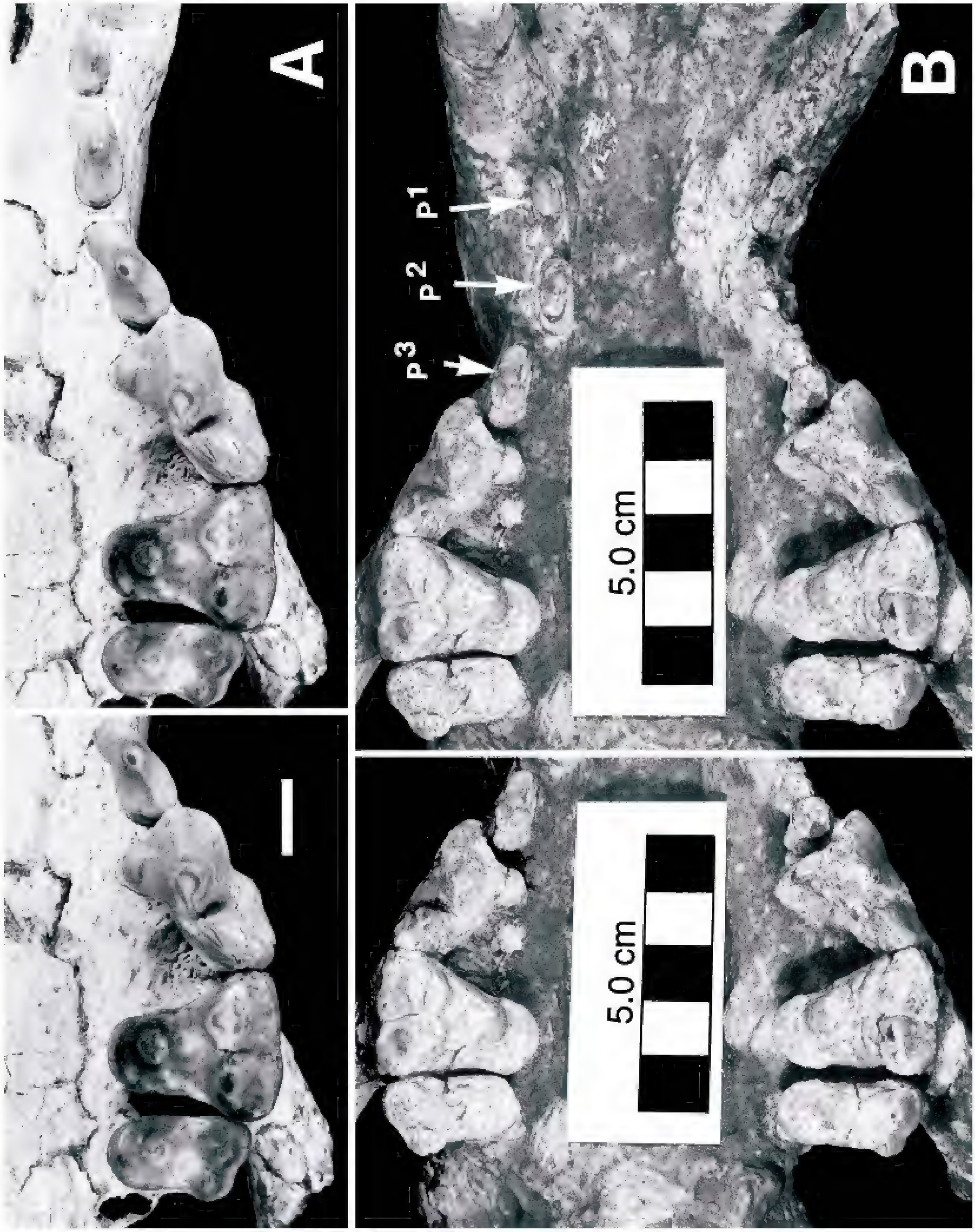
Fig. 8. Lower molar dimensions (m1, m2, length and width in mm) of North American *Ysengrinia americana* and European species of *Ysengrinia*. A sample of the latest Arikareean amphicyonid *Daphoenodon superbus* is included to demonstrate the extent of variation in these measurements in a single species from a limited stratigraphic interval. Statistical data for *D. superbus*, m1 length and width (N = 13): range, 24.2–27.4 mm, 11.1–12.0 mm; mean, 25.6, 11.5 mm; 1 SD, 0.93, 0.25. *D. superbus*, m2 length and width (N = 8): range, 13.9–17.4 mm, 9.8–11.5 mm; mean, 15.1, 10.4 mm; 1 SD, 1.20, 0.57.

of p4. The p4 in *Y. americana* lacks the nearly rectilinear mesial face of *Y. tolosana* and is longer relative to m1 length than in most *Y. tolosana* and *Crassidia intermedia* (p4/m1 ratio, *Y. americana*, 0.66–0.71; *Y. tolosana*, 0.61; *C. intermedia*, ~0.62; however, the Flörsheim mandible of *Y. tolosana* has a ratio of ~0.70, based on measurements in Kuss, 1965). In the *Y. americana* paratype (F:AM 54147), a fine enamel ridge runs from the principal cusp of p4 directly to the anterior edge of the tooth and is not diverted toward the lingual face as in *Y. tolosana*; in other *Y. americana* individuals the ridge is more similar in its course to *Y. tolosana*. *Ysengrinia tolosana* also tends to have a wider m2 than *Y. americana* (fig. 8).

DESCRIPTION: The paratype cranium is the only complete skull of the genus (figs. 3, 6). It is distinguished from its contemporary, *Daphoenodon*, by larger size, greater basilar length of the skull (~30 cm), short snout with reduced premolars, and by the relatively small braincase surmounted by a long, dorsoventrally prominent sagittal crest. Before it was recognized as *Ysengrinia*, several investigators commented on the "primitive" appearance of the skull: the small volume of the braincase is remarkable relative to the size of the skull, resulting in a particularly prominent sagittal crest for attachment of massive temporal muscles, and an exceptionally low occipital region of very small area. The frontal region is only moderately inflated and its surface is not domed, but is rather flat. The basicranium is anteroposteriorly short, but is poorly preserved, revealing little detail; the mastoid processes were at least moderately developed. The auditory bulla was evidently ossified and of small volume, with a laterally prolonged bony external auditory meatus ~1 cm in length.

The dentitions of the holotype palate (fig. 5) and paratype skull (fig. 9), with its associated deep, robust mandible, show that *Y. americana* had reduced anterior premolars. This differs from the species of *Daphoenodon* and the large contemporary temnocyonine amphicyonids of the early Miocene, all of which retain fully developed premolars.

In North America there is only a single individual (F:AM 54147, paratype) with an associated upper and lower dentition (figs. 3, 9B). The skull has a short rostrum, broad-


A
B
P1
P2
P3
5.0 cm
5.0 cm

ened at the level of the large canines, an expanded frontal region, and a small braincase relative to overall cranial size. M1–2 in the paratype and holotype are particularly diagnostic (figs. 5, 9); isolated M1s of this type are also reported from the American Museum–Cook Quarry and Morava Ranch Quarry (Hunt, 1972: fig. 10A, B). M2 is not enlarged relative to M1. M1 is transversely extended, forming an isosceles triangle in occlusal view, with a distinctive lingual cingulum characteristic of the North American species. The cingulum is thin anterior to the protocone but is thickened and enlarged lingual and posterolingual to that cusp. A shallow basin separates the thickened posterolingual cingulum from the base of the protocone. The M1 paracone is taller than the metacone; its anterolingual face has a prominent wear facet (F:AM 25420) produced by shear against the posterior surface of the m1 trigonid. In older individuals this cusp cuts a deep groove in the labial face of the m1 talonid (visible in paratype m1). The protocone forms the lingual apex of a V-shaped platform whose arms surround a shallow protocone basin. The arms of the V continue laterad as thin ridges (pre- and postprotocristae) to the bases of the paracone and metacone. The paraconule and metaconule are either absent or only weakly developed. The enlarged metaconule of *Amphicyon* does not occur. M1 is similar in form to the holotype M1 of "*Amphicyon*" *intermedius* from the German Aquitanian (Kuss, 1965: fig. 75, SMNS 4568), recently designated the holotype of *Crassidia intermedia* (Heizmann and Kordikova, 2000), but differs in occlusal details.

M2 is smaller than M1, subrectangular, and transversely extended by an expanded lingual cingulum. The metacone is smaller than the paracone, less so in the holotype M2, more so in stratigraphically younger individuals (F:AM 54147), suggesting a possible trend toward reduction of M2–3 in time. The protocone forms the lingual apex of a low V-shaped platform which is surrounded by the thickened tonguelike lingual cingulum. M2 varies in anteroposterior length in different individuals but not in the pattern of its cusps.

M3 is preserved only in the holotype, where it is markedly smaller than M2. The paracone, metacone, and protocone are very low cusps, the metacone reduced relative to the others. M3 is surrounded by a distinct cingulum, thicker lingually and in the parastylar area.

P4 is a relatively narrow shearing carnassial with a low but distinct protocone. The most distinctive feature of P4 in the holotype is a fine enamel ridge that descends the anterior face of the paracone to the cingulum. Labial to this point of contact the cingulum is conspicuously thickened as a pseudoparastyle. Although P4 is known only in the holotype and paratype of *Y. americana*, it differs from the relatively shorter, more robust P4 of New World *Amphicyon* which invariably displays a true parastylar cusp at the base of the paracone. M1 length/ P4 length ratios of the para- and holotype of *Y. americana* are 0.76 and 0.82, respectively, whereas in early Hemingfordian *Amphicyon* (F:AM 25400, UNSM 1570-59) this ratio is 0.92.

P1–3 are reduced in *Y. americana*, decreasing in size from P3 to P1, each with a low, central cusp and no accessory cusps (fig. 9B). P2–3 each have two roots; P1 is single-rooted. P3 in the holotype shows a selective thickening of the cingulum at the anterior and posterior ends of the tooth, and also a sharp crease in the enamel of the posterolingual face that continues into the cingulum. P3 in *Y. americana* is taller and somewhat narrower than P3 in *Amphicyon*. There are short diastemata between P1–P2 (~5–6 mm) and P2–3 (~7 mm). The snout is conspicuously narrowed at the level of P2.

←

Fig. 9. **A,** Upper dentition of a daphoenine amphicyonid, F:AM 27568, Upper Harrison beds, 18 Mile District, Goshen County, Wyoming. This species with developed premolars is representative of all other Upper Harrison amphicyonids in contrast to the reduced premolars of *Ysengrinia*. Scale bar, 1 cm. **B,** Upper dentition of *Ysengrinia americana*, paratype, F:AM 54147, Upper Harrison beds, 25 Mile District, Goshen County, Wyoming. Note reduced premolars 1–3.

Fig. 10. Stereophotographs of unworn right upper canine, *Ysengrinia americana*, UNSM 44670, Harper Quarry, latest Arikareean, Sioux County, Nebraska. Lateral view. Scale bar, 1 cm.

Upper and lower canines of the paratype are robust teeth, blunted by heavy wear. Abrasion by the lower canine has produced a flat wear surface along the length of the anterointernal face of the upper canine. The posterior face of the lower canine is reciprocally grooved by the upper canine, and the anterointernal face of the lower canine is deeply worn by the action of the large I3. An unworn upper canine (fig. 10) from Harper Quarry is 103 mm in length; at the crown base the anteroposterior length is 23.3 mm, and width is 17.4 mm; crown height is 45.8 mm. Thin sharp enamel ridges traverse the length of the posterior and anterolingual faces of the upper canine. This canine is identical in form and size to the unworn upper canine of the holotype (YPM 10061). The anteriorly deep, massive mandible of *Y. americana* (F:AM 54147, F:AM 25423) is in part the product of the development of robust canines in this carnivore.

The incisors are evident only in the paratype. I3 is large but blunted by heavy wear. I2, much smaller than I3, exists only as a broken root; I1 was present but was lost from the premaxilla.

The mandible is represented by the paratype (fig. 7) and a previously described edentulous mandible (F:AM 25423) from Morava Ranch Quarry (Hunt, 1972: figs. 8, 9). The depth of the paratype mandible is remarkable: 56 mm below the m2 trigonid, 50.7 mm below p2 (the holotype of *Daphoenodon superbus*, a female, CM 1589, measures 30.3 and 24.5 mm, respectively; a large male *D. superbus*, UNSM 700-82, measures 38.6 and 29.5 mm). Both the holotype and F:AM 25423 have a broad shallow trough, ~2 cm in greatest width, extending along the length of the internal surface of the mandible from below p3 to a short distance behind m3. The considerable force developed by the masseter complex during occlusion of the carnassials and molars is indicated by the deep masseteric fossa bordered by conspicuously thickened ventral and anterior margins of the ascending ramus. A rugose angular process projects backward and is deflected medially. Only the medial half of the robust articular condyle is preserved; it is placed at the level of the toothrow.

Characteristic of the species are two large close-spaced mental foramina ~1 cm apart on the labial surface of the mandible: the posterior foramen occurs below the anterior root of p3, the anterior foramen below p2.

A partial mandible of *Y. americana* (fig. 11, UNSM 26584) from UNSM locality Sf-105 lacks the ascending ramus and ventral border so that the depth of the jaw cannot be determined. However, p3–m2 are well-preserved and unworn (fig. 12) and show a marked similarity to these teeth in *Y. tolosana* (NMB Pa 951) from Paulhiac. Both in UNSM 26584 and in the paratype, p1–3 are reduced in size relative to the posterior cheek teeth. Only alveoli and roots are preserved in the paratype, but their size and spacing indicate that they progressively diminished in size from p3 to p1. The p2 was a very small (length, 8.5 mm in paratype; alveolus length, 6.2 mm in UNSM 26584), low, elliptical tooth with a single apical cusp.

The paratype p4 is an elongate premolar whose posterior margin contacted the carnassial. The prominent central cusp is flanked

Fig. 11. *Ysengrinia americana*, partial right mandible with p3–m2, UNSM 26584, Harrison Formation, late Arikareean, Scottsbluff County, Nebraska. **A,** lateral view; **B,** medial view. Scale bars, 1 cm.

by a strong posterior accessory cusp and a low heel with a small cingulum cusp. A thin enamel ridge runs down the anterior face of the tooth to a weak enamel swelling. The profile of the anterior face is not rectilinear as in *Y. tolosana*, but is mesially extended. This tooth is the most variable in the dentition: in UNSM 26584 the p4 is short and rather broad (fig. 12), and in UNSM 7131-83 the p4 is intermediate in length and width, falling between the short, broad p4 of UNSM 26584 and the more elongate p4 of F:AM 54147. Illustrations of p4 in European species also seem to show this variation.

The m1 is robust with a tall trigonid and low wide talonid. The paraconid is placed directly anterior to the tall protoconid; the prominent metaconid is somewhat retracted posterolingual to the protoconid. Although the talonid is heavily worn in the paratype, an m1 talonid from Harper Quarry (UNSM 44671, fig. 13A) and a complete m1 from UNSM Loc. Sf-105 (fig. 12) are unworn and show a blunt swollen hypoconid ridge bordered internally by a short shelf with a very weak entoconid. In the paratype m1, the posterolabial face of the tall protoconid and adjacent anterolabial part of the talonid display a deep wear groove produced by action of the M1 paracone. The marked size difference between the m1 of the paratype and UNSM 44671 suggests that the teeth of *Y. americana* are sexually dimorphic.

Occlusion of P4, M1, and m1 result in a number of vertically oriented shear surfaces that demonstrate a slicing action. Crushing is simultaneously accomplished by occlusion of M1–2 with m2–3 and the m1 talonid. Verti-

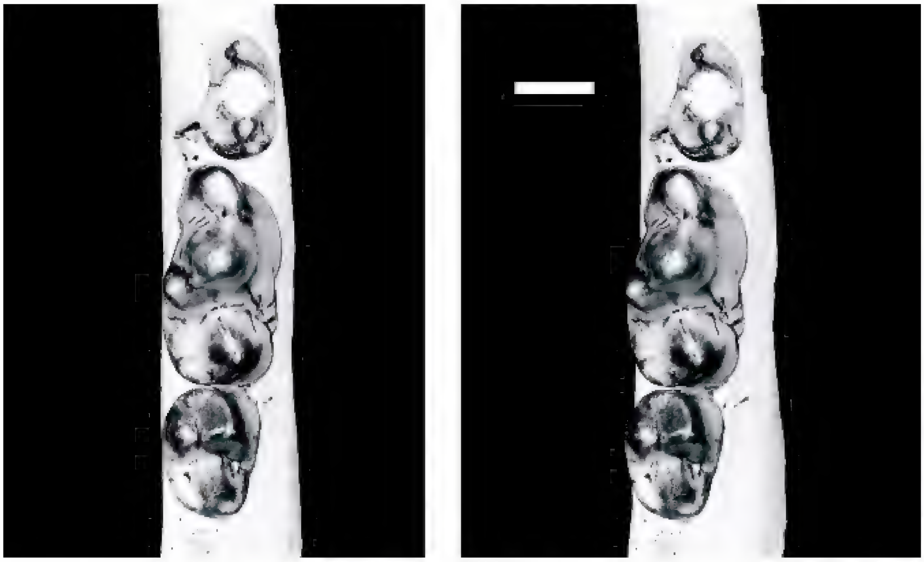


Fig. 12. *Ysengrinia americana*, occlusal view of p4–m2, UNSM 26584, Harrison Formation, late Arikareean, Scottsbluff County, Nebraska. Stereophotographs. Scale bar, 1 cm.

cal wear surfaces associated with carnassial shear, and the depth of the wear groove along the labial face of m1 produced by the M1 paracone, are better developed than in North American early Miocene *Amphicyon*.

The m2 is subrectangular with a broad trigonid and narrower talonid; m2 is not elongated relative to m1 (figs. 7, 11, 12, 13B). The m2 trigonid occupies the anterior half of the tooth and is not crowded to the front of the tooth, as in *Pseudocyon*. The protoconid is the most prominent cusp, connected by a smooth enamel arc to the low paraconid ridge. A low rounded metaconid is separated from the protoconid by a distinct crease in the enamel. The m2 trigonid surface forms a shallow basin sloping linguad. The m2 talonid is a low platform with a labially placed hypoconid ridge. The internal surface of the hypoconid slopes toward the lingual edge of m2; there is no talonid basin or entoconid. The form of m2 in *Y. americana* is nearly identical to m2 of Paulhiac *Y. tolosana* (NMB Pa 951); the lower dentition of these two species is extremely similar.

The m3 is elliptical, robust, with an irregular surface of nearly uniform height on which individual cusps are no longer distinct. The m2–3 and m1 talonid together form a crushing platform ~35 mm in length in the paratype.

Comparison of New and Old World Species

A comparison of *Y. americana* with the European species of *Ysengrinia* is essentially limited to the lower dentition and mandible because European holotypes of *Y. tolosana, Y. gerandiana*, and *Y. depereti* are mandibles without associated upper teeth. No population samples in Europe allow us to adequately assess dental variation within a species, and no postcrania have been attributed to the genus with certainty. All *Ysengrinia* species apparently show a modest reduction of the anterior premolars (p1–3), a trait common to many amphicyonines. Because p1–4 are not preserved in the holotype mandible of *Y. depereti*, this inference is based on the size of premolar alveoli. The *Y. tolosana* holotype lacks the anterior part of the mandible but the referred mandible from Paulhiac (NMB Pa 951) shows reduced anterior premolars. Thus, identification of *Ysengrinia* rests heavily on p4–m3.

North American *Y. americana* shares certain dental and mandibular traits with the European *Y. tolosana*. In particular, m1–m2 of

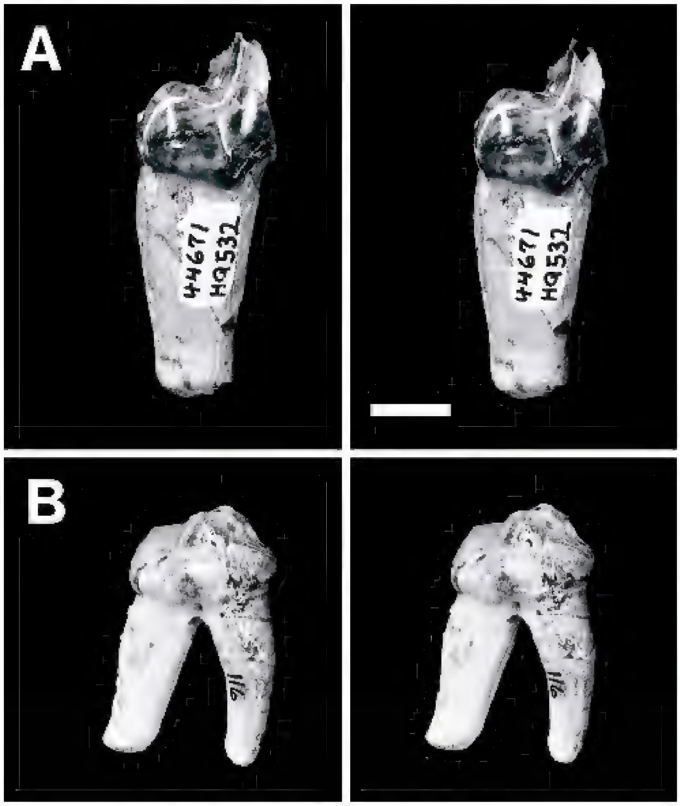


Fig. 13. *Ysengrinia americana*: **A,** m1 talonid, right (labial view), UNSM 44671; **B,** isolated m2, right (labial view), UNSM 44673, both from Harper Quarry, latest Arikareean, Sioux County, Nebraska. These are the largest molars attributed to *Y. americana* and probably belong to a male. Scale bar for both molars, 1 cm.

the *Y. americana* paratype (F:AM 54147), and the m1–m2 of a referred mandible (UNSM 26584), are nearly identical in form and dimensions to these teeth in Paulhiac *Y. tolosana* (NMB Pa 951) described by Bonis (1973). To estimate dental variation expected in a single amphicyonid species contemporaneous with *Ysengrinia*, m1 (N = 13) and m2 (N = 8) dimensions were plotted for *Daphoenodon superbus*; this sample comes from a limited stratigraphic interval in the lower part of the Upper Harrison beds, Sioux County, Nebraska. Figure 8 shows these measurements for *D. superbus*, *Y. americana*, and the European species of *Ysengrinia*. The m1–m2 measurements of *Y. americana* are closely grouped with those of *Y. tolosana* and *Y. gerandiana*, and could be regarded as within the expected range of a somewhat variable species. However, details of the lower dentition and the shape of the mandibles indicate that these are distinct species.

The p4 in the *Y. americana* paratype from the Upper Harrison beds is longer than the short p4 of Paulhiac *Y. tolosana* (NMB Pa 951), and it lacks the rectilinear profile of the Paulhiac p4. However, *Y. americana* from the Harrison Formation (UNSM 26584) also has a short p4. The *Y. americana* paratype p4 appears more similar in form to p4 of the Flörsheim *Y. tolosana* mandible (Kuss 1965: fig. 55). It seems that *Y. americana* and the European species include both short, wide p4s and more elongate, narrow p4s; until a larger number of individuals from a single stratigraphic level is available, the explanation of this variation in p4 remains uncertain.

The *Y. depereti* holotype from Chilleurs-aux-Bois (MN3b, Mus. Orléans 785) is dis-

tinguished from *Y. americana* by its larger m2. Also, the principal cusps of the *Y. depereti* m2 terminate in sharp, anteroposterior crests, and the protoconid and metaconid are joined by thin transverse enamel crests; in *Y. americana* (F:AM 54147, UNSM 26584) and in *Y. tolosana* (NMB Pa 951) these cusps are more rounded and the crests less sharply defined. In *Y. depereti* the m2 protoconid and metaconid are joined anteriorly by a low arcuate enamel rim that forms the anterior border of this tooth; the two cusps and the rim surround a well-defined trigonid basin. *Ysengrinia americana* (F:AM 54147, UNSM 26584) and *Y. tolosana* (NMB Pa 951) lack this defined basin of *Y. depereti*, and have a shallower trigonid basin the margins of which blend smoothly into the peripheral cusps. The m2 of *Y. americana* and *Y. tolosana* are narrower than the broad m2 of *Y. depereti*. The two former species also have a hypoconid that fills most of the talonid, leaving only a narrow inner talonid margin. In *Y. depereti* the wider m2 talonid has a labially restricted, sharp hypoconid ridge, bordered lingually by a broad, low talonid shelf.

There is an evident affinity shared by the teeth of *Y. americana* and *Y. tolosana*, and among the m2s of *Y. americana*, *Y. tolosana*, and *Y. gerandiana*. However, given our incomplete knowledge of the upper dentition, skull, and postcranial skeleton of the European species, speculation about the relationships among these nominal species is premature.

POSTCRANIAL OSTEOLOGY

Postcranial bones of *Ysengrinia* were well represented at the Harper Quarry waterhole bonebed, Sioux County, northwest Nebraska (Hunt, 1978). Also, a partial forelimb was associated with the *Y. americana* paratype cranium and mandible (FAM 54147) from the 25 Mile District, and an associated partial hindlimb (USNM 186993) was found west of Spoon Butte, both from Goshen County, southeastern Wyoming.

The morphology of the foot and limb bones shows some similarities to those of large living ursids. However, the proportions of the epipodial (radius, tibia) to propodial (humerus, femur) elements are more similar to those of living lions (*Panthera leo*, table 2). Although there is no association of a complete radius or ulna with the humerus of *Y. americana*, F:AM 54147 includes two proximal ulnae, a distal radius, and a complete humerus from one individual that can be used to estimate forelimb proportions. The humeroradial index (Davis, 1964: 93) calculated for F:AM 54147 is ~89.3, and for the largest unassociated humerus and radius from Harper Quarry it is 90.6. These values are most similar to humeroradial indices of living lions (90.0–94.0, table 2). Although the radius of *Y. americana* is shorter than the humerus, its humeroradial index exceeds the range of the index for living ursids (78.3–86.3) and tigers (*P. tigris*, 80.7–86.4), demonstrating a relatively longer lower forelimb in *Ysengrinia* and in living lions.

However, a shorter lower hindlimb in *Ysengrinia americana*, relative to lions (83.7–89.3) and tigers (83.4–87.6), is reflected in the femorotibial index of 79.8 for the only known associated hindlimb (USNM 186993). Using the median values for the lengths of all *Y. americana* femora and tibiae, the femorotibial index is <82, whereas in lions and tigers it is >82. On the other hand, *Y. americana* has a somewhat longer tibia relative to those of living North American *Ursus americanus* (71.4–75.9), *Ursus arctos* (68.2–71.9), the large Kodiak Island *Ursus* (67.9–73.9), and the polar bear *Thalarctos* (73.9–74.4). Thus, the lower limb (epipodial) segments in *Ysengrinia* appear to be somewhat longer than those of the living North American bears.

The humeroradial and femorotibial indices of *Ysengrinia* describe a heavily muscled, short-footed carnivore without cursorial specializations of the limbs and feet. In cursorial canids (*Canis lupus*, *C. latrans*, table 2) the humeroradial index ranges from 97.2 to 104.4, and the femorotibial index from 96.5 to 100.9. In the long-legged *Chrysocyon brachycrus* of South America, both indices exceed 100. Thus, *Ysengrinia* was not proportioned as in living larger cursorial carnivorans such as wolves, but more closely approached the limb indices of the large cats. However, *Y. americana* differed from them in lacking their more elongate tibia and tarsus.

SCAPULA: An enormous scapula associated with the partial hindlimb (USNM 186993) from the Lay Ranch beds west of Spoon Butte, Wyoming, measures 28 cm from the dorsal border of the glenoid to the point where the scapular spine intersects the vertebral border (fig. 14A). The scapular spine is extremely broad, ~3 cm in height at its midpoint; it terminates inferiorly in a well-developed acromion and more subdued metacromion process. Internal to the acromion the base of the scapular spine is broadened to enclose the suprascapular artery and nerve within a bony foramen. This foramen is not present in large ursids or felids in which the artery lies anterior to the edge of the scapular spine without bony enclosure. The large species of *Panthera* show moderate development of the acromion and metacromion, but *Ysengrinia* is most similar to *Ursus arctos*, *U. americanus*, and *Thalarctos maritimus* in which the metacromion is not well differentiated.

The outer surface of the scapula reflects the great mass and thickness of the muscles of the rotator cuff that stabilized the huge shoulder of *Ysengrinia*. Despite breakage, a prominent postscapular fossa for the subscapularis muscle, similar to that in ursids, was present along the caudal margin of the scapula at its junction with the vertebral border. The ventral border of the scapula is thickened and laterally reflected to accommodate the subscapularis minor within a broad shallow sulcus along its ventral margin. Within the infraspinous fossa an elliptical muscle scar 7.5 cm in length and 2.5 cm in greatest width, placed slightly posterior to the midpoint of the fossa, may have contained a separate belly of infraspinatus—no similar scar occurs in ursids or felids.

Dimensions of the glenoid fossa of the scapula convey a sense of the mass of the forequarters of these large carnivorans (table 3). The glenoid area of *Ysengrinia americana* is similar to that of some *Thalarctos maritimus*, falling below the dimensions of large *Ursus arctos* but above those of *Panthera leo* and *P. tigris*.

HUMERUS: The humerus was previously described (Hunt, 1972: 16f.), based on a well-preserved example (CM 2400) collected by O.A. Peterson (1910) east of the Agate quarries (fig. 15). The humerus is similar to that of large ambulatory ursids which can move swiftly over short distances, and which retain considerable mobility of the forelimb. The bone is robust, including a particularly massive diaphysis, created in part by the insertion of brachialis (long head), cephalohumeralis, and pectoral muscles along the deltoid-pectoral crests to produce a broad surface of attachment that extends for 20 cm along the anterior face of a humerus 30 cm in length. The distal end of the humerus is transversely widened as in ursids by well-developed lateral and medial epicondyles continuous with the supracondylar ridges for the origin of major extensors and flexors of the wrist and digits. The medial epicondylar region is developed as a rugose process, and as a result the shallow olecranon fossa of *Y. americana* is somewhat extended medially. A similar asymmetric olecranon fossa is present in living *Ursus* and in North American early Miocene *Amphicyon* but the fossa is deeper and more dorsally extended than in *Ysengrinia*. The deep olecranon fossa of *Ursus* and *Amphicyon* allows a more secure locking of the anconeal process of the ulna in the fossa—the contact of the lateral face of the anconeal process with the side of the olecranon fossa creates a bony stop mechanism that prevents lateral bending of the elbow joint. *Ysengrinia americana* has a somewhat more primitive articulation of distal humerus with ulna.

Ysengrinia retains an entepicondylar foramen for the brachial artery and median nerve, whereas in living *Ursus* the bony bar enclosing the vessel and nerve is lost and the foramen is open medially.

RADIUS-ULNA: The radius and ulna of *Y. americana* are known from complete specimens at Harper Quarry (fig. 16). The paratype skeleton includes only a distal radius and proximal parts of the two ulnae (fig. 17); however, they compare with the Harper Quarry elements. The radius and ulna are similar to these bones in large living ursids and felids but there are some noteworthy differences. The massive construction of radius and ulna, the thick diaphyses, and prominent rugosities for interosseous ligaments indicate the powerful muscular forces transmitted to the lower limb skeleton. The radii of *Ursus*

TABLE 2
Limb Bone Lengths (in mm) and Limb Proportions of the North American Amphicyonid *Ysengrinia americana* Compared with Other Amphicyonids, and Living Ursids, Felids, and Canids

	Humerus	Radius	R/H[a]	Femur	Tibia	T/F[b]
AMPHICYONIDAE						
Daphoenus vetus						
F:AM 50329	168	129	76.8	193	172	89.1
F:AM 25451	142	119	83.8	—	—	—
AMNH 11857	165	138	83.6	—	—	—
CM 492	185	135	73.0	201	179	89.0
Daphoenodon superbus						
CM 1589	210	182	86.7	230	205	89.1
Ysengrinia americana						
CM 2400	300	—	—	—	—	—
UNSM 44606	287	—	—	—	—	—
F:AM 54147	270	241[c]	89.3	—	—	—
USNM 186993	—	—	—	351	280[c]	79.8
UNSM 44600	—	260	—	—	—	—
UNSM 44601	—	250	—	—	—	—
UNSM 44691	—	252	—	—	—	—
UNSM 44624	—	—	—	364	—	—
UNSM 44690	—	—	—	353	—	—
UNSM 44620	—	—	—	—	287	—
UNSM 44621	—	—	—	—	297	—
UNSM 44622	—	—	—	—	287	—
UNSM 44623	—	—	—	—	288	—
Cynelos lemanensis[d]	220	197	89.5	282	240	85.1
URSIDAE						
Ursus arctos[e]						
CNHM 43744	304	247	81.2	355	248	69.9
CNHM 47419	312	255	81.7	377	253	68.2
CNHM 84467	204	162	79.4	249	179	71.9
Ursus arctos (Kodiak)						
ZM 17888	405	334	82.5	448	331	73.9
CNHM 63802	415	345	83.1	519	355	68.4
CNHM 27268	386	305	79.0	464	315	67.9
CNHM 63803	327	268	82.0	390	275	70.5
Ursus americanus						
CNHM 18864[e]	244	191	78.3	276	197	71.4
CNHM 44725[e]	286	225	83.9	318	232	72.9
AM 24157	334	282	84.4	370	281	75.9
Thalarctos maritimus						
AM 75244	394	340	86.3	465	346	74.4
AM 75245	385	325	84.4	453	335	73.9
FELIDAE						
Panthera tigris						
ZM 14343	296	242	81.8	334	285	85.3
ZM 14602	270	225	83.3	314	262	83.4
ZM 14603	274	221	80.7	—	—	—
AM 217100	301	260	86.4	345	296	85.8
AM 14030	267	226	84.6	301	261	86.7
AM 14032	298	250	83.9	340	291	85.6
AM 85404	344	289	84.0	398	347	87.2
AM 85396	345	287	83.2	398	349	87.6
AM 135846	313	265	84.7	348	300	86.2

TABLE 2
(*Continued*)

	Humerus	Radius	R/H[a]	Femur	Tibia	T/F[b]
FELIDAE (continued)						
Panthera leo						
AM 85140	324	298	94.0	361	307	85.0
AM 85142	303	285	94.0	350	298	85.1
AM 85143	323	300	92.9	369	309	83.7
AM 85144	328	295	90.0	369	317	85.9
AM 85145	296	278	93.9	344	297	86.3
AM 85147	289	265	91.7	323	275	85.1
AM 85149	330	302	91.5	368	322	87.5
AM 52078	369	333	90.2	404	339	83.9
AM 80609	332	311	93.7	372	320	86.0
AM 54995	322	293	91.0	360	320	88.9
AM 54996	301	273	90.7	338	302	89.3
CANIDAE						
Canis lupus[e]						
CNHM 21207	209	213	101.9	234	233	99.6
CNHM 51772	228	227	99.6	255	246	96.5
CNHM 51773	216	210	97.2	241	233	96.7
CNHM 54015	209	207	99.0	230	232	100.9
Canis latrans						
Davis, 1964: 35[e]	—	—	104.4 (3)[f]	—		99.6 (3)
Chrysocyon brachyurus						
Davis, 1964: 35[e]	—	—	108.1 (2)	—		107.8 (2)

[a] Humeroradial index (Davis, 1964).
[b] Femorotibial index (Davis, 1964).
[c] Estimated.
[d] From Ginsburg (1977).
[e] From Davis (1964).
[f] ( ) Indicates sample size.

and large *Panthera* all show a strong curvature of the diaphysis; in *Ysengrinia* the massive columnar radius has almost no curvature. The articulation of the distal humerus with the radius-ulna is most similar to the configuration in living ursids. The smoothly concave radial notch of the ulna and the convex articular margin of the radial head indicate a degree of rotation of the radius around the ulna (supination-pronation) similar to large ursids. A massive subrectangular radial tuberosity for attachment of the biceps tendon suggests the power of this rotation. Muscle scars for the interosseous ligaments are particularly developed. The radius and ulna differ from those of early Hemingfordian North American *Amphicyon* in that the radius of the latter is more slender and not as massive, and its proximal ulna fits more deeply into the olecranon fossa of the humerus—this is apparent from the greater dorsal extent of the articulation surface on the lateral face of the anconeal process in *Amphicyon*. Similarly, in *Ursus* the lateral articulation surface of the anconeal process extends far dorsad, nearly to the tip of the olecranon process. In *Y. americana*, however, the articulation surface on the lateral face of the anconeal process does not extend as far dorsad as in *Amphicyon* and *Ursus*. None of the *Ysengrinia* radii possess a radial exostosis like that known for *Daphoenodon* and *Daphoenus*.

CARPALS: The carpus is represented by left and right scapholunars (fig. 18) and by a right unciform from Harper Quarry: all are heavy, massive bones, indicating the considerable force transmitted through the forelimb. A scapholunar of the same type is also

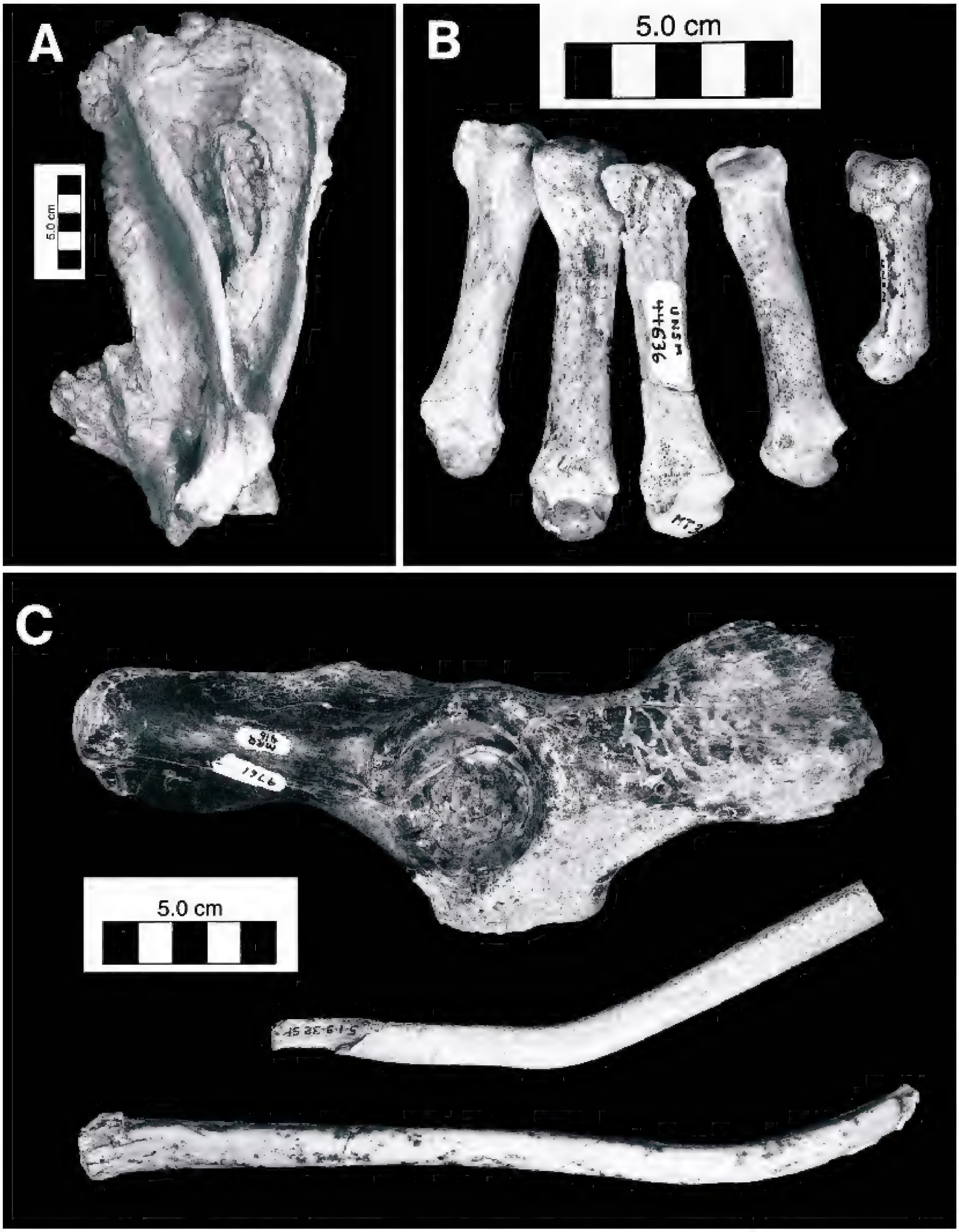


Fig. 14. **A,** Left scapula of *Ysengrinia americana*, USNM 186993, Lay Ranch beds, west of Spoon Butte, Goshen County, Wyoming, associated with femur-tibia of figure 20. **B,** Metatarsals 1–5 of a composite pes, *Y. americana*, Harper Quarry, Upper Harrison beds, Sioux County, Nebraska. From right to left: MT1, UNSM 44640; MT2, UNSM 44639; MT3, UNSM 44636; MT4, 44638; MT5, UNSM 44634. **C,** Right innominate (above), *Y. americana*, ACM 9761, Morava Ranch Quarry, Box Butte

present in the paratype (fig. 19). The dorsal surface of the scapholunar is smoothly convex, without diagnostic features. However, the ventral surface displays a distinctive topography that can be compared with that of ursids and large felids, produced by the articulations with the unciform, magnum, trapezoid, and trapezium.

In living *Ursus*, three facets on the ventral surface can be recognized: an unciform facet and magnum facet are sharply demarcated, are aligned fore-aft, and occupy the lateral half of the ventral surface; a conjoined quadrate facet for trapezoid-trapezium is confined to the medial half of this surface. In *Panthera leo* and *P. tigris* the unciform and magnum facets are crowded to the lateral side of the scapholunar, leaving a large triangular area for the trapezoid-trapezium articulation. The pattern of facets on the ventral surface of the *Ysengrinia* scapholunar (fig. 19A, B) is similar to *Panthera* and is distinct from the derived pattern found in *Ursus*. In addition, in *Ursus* the trapezoid is smaller than the trapezium, but in *Panthera* the trapezoid is larger. In the lion the trapezoid extends along the front of the scapholunar to the medial border, hence the trapezium is restricted to the posteromedial corner of the scapholunar. In *Ursus*, however, the trapezoid lacks this medial extension, and the trapezium intervenes at the anteromedial corner of the scapholunar.

The unciform was also preserved at Harper Quarry: its geometry and facet pattern are most like large extant species of *Ursus*. A pisiform was associated with the partial skeleton from Spoon Butte; it conforms exactly to this bone in large *Ursus*. It is of interest because the ligament thought to be responsible for a prominent elliptical scar on the posterior surface of metacarpal 4 originates from the pisiform (fig. 18, see below).

METACARPALS: Metacarpals 2 and 4 were found at Harper Quarry, metacarpals 1 and 3 were not; however, there are five fifth metacarpals, including four of the right side. The distal surface of the unciform is broad and smoothly concave, articulating with the proximal ends of the large metacarpals 4 and 5. Metacarpal 5 determines the minimum number of individuals (N = 4) of *Ysengrinia* present in Harper Quarry, and also demonstrates dimorphism in the foot: UNSM 44611 and 44615 are about the same length, but the former (female) is gracile whereas the latter (male) is much thicker and more robust (fig. 18A, B). The greatest width of the proximal end of metacarpal 5 in these individuals is 25.2, 23.7, 23.3, 23.0, and 22.9 mm. It is a short robust bone, comparing in anatomical detail to the metacarpal 5 of ursids, but in living ursids and large felids the bone is much longer than in *Ysengrinia*.

Metacarpal 1, clearly reduced in size, is associated with the paratype cranium and mandible (F:AM 54147). Although metacarpal 3 is not known, the reduced size of metacarpal 1 and the lengths of the fifth metacarpals suggest that the forefoot was probably paraxonic.

The metacarpals (figs. 18A–D, 19C, D) demonstrate that *Ysengrinia* had a short forefoot. Anatomical details of the metacarpals are extremely similar to those of living ursids such as *Ursus arctos* and *U. americanus*. Metacarpal 2 from Harper Quarry is most similar to this bone in *Ursus*. The strongly developed interlocking overlap of the edge of metacarpal 2 on metacarpal 3 seen in large felids is not present in *Ysengrinia*. Similarly, the facets of the proximal end of metacarpal 4 duplicate those of *Ursus* and differ from those of large felids. In one important anatomical detail, *Ysengrinia* metacarpals differ from those of *Ursus*. In ursids a prominent elliptical scar occurs on the posterior surface of the diaphysis of metacarpal 4 immediately below the articular head; this scar is always situated above the midpoint of the diaphysis of the metacarpal. In amphicyonids it occurs more distally on the shaft of the metacarpal where it is closer to the midpoint of the diaphysis, often extending below it. The scar apparently represents an attachment for a lig-

←

County, Nebraska; baculum of large undescribed amphicyonid (middle), UNSM 5-1-9-32SP, Bridgeport Quarries, Morrill County, Nebraska; baculum (below), UNSM 44629, length, 24 cm, *Y. americana*, Harper Quarry, Upper Harrison beds, Sioux County, Nebraska.

TABLE 3
Comparative Measurements (in mm) of the Scapula in North American Early Miocene Amphicyonids and Large Living Ursids and Felids

	A-P diameter of glenoid[a]	Transverse diameter of glenoid	Museum number	Sex
Amphicyonidae				
Daphoenodon superbus	39	24	CM 1589	F
Ysengrinia americana	71	44	USNM 186993	?
Ursidae				
Ursus americanus	55	33	UNSM 283	?
U. americanus	51	30	UNSM 3253	F
U. americanus	50	28	UNSM 16986	F
U. americanus	45	27	UNSM 15112	?
Helarctos malayanus	37	23	UNSM 13875	F
Ursus arctos (Brown)	83	43	UNSM 19565	M
U. arctos (Kodiak)	95	48	UNSM 17888	M
Thalarctos maritimus	85	50	UNSM 16938	M
T. maritimus	70	47	AM 75244	?
Felidae				
Panthera tigris (Siberia)	64	42	UNSM 16656	M
P. tigris (Sumatra)	57	35	UNSM 14343	?
P. tigris (Sumatra)	49	32	UNSM 14602	?
Panthera leo	64	42	UNSM 14278	M
P. leo	60	41	UNSM 15480	?

[a] A-P = anterior-posterior.

ament of the carpus (the medial distal accessory ligament of canids running from the pisiform to metacarpal 4 may be comparable: see Miller et al., 1964: 225), which joins an accessory carpal bone (pisiform) to the palmar aspect of metacarpal 4.

PHALANGES: Because the available phalanges are not associated with metapodials, it cannot be determined whether they belong to the fore- or hindfoot. Considered as a group, the 17 phalanges from Harper and Morava Ranch quarries are similar to those of large ursids. The proximal phalanges are particularly massive and broad. Intermediate phalanges are smaller and more dorsoventrally compressed; they display a strong process at the center of the dorsal edge of the proximal end for attachment of the extensor tendons of the digits, and the ventral surface is flat. The smaller intermediate phalanges show a moderate degree of asymmetry not seen in the large ones; the large intermediate phalanges belong to the central digits 3–4 whereas the smaller are those of the side toes. There is no evidence of retractile claws. The ungual phalanges were not preserved.

VERTEBRAE: Vertebrae were found only at Harper Quarry. There were a large number of lumbar vertebrae (N = 11), but only two of the atlas, one cervical and one thoracic. This may be due to the destruction of the rib cages and thoracics during scavenging of the carcasses at the waterhole.

The lumbars have elongate centra as in *Panthera*, unlike the short ones of living ursids. Although the transverse processes are mostly broken, some show the downward sweep typical of large *Panthera*, whereas others are directed more laterad as in ursids. However, the base of these processes tends to be situated lower on the centrum than in ursids, much as in large living felids. Large accessory processes also occur on the anterior lumbars of *Ysengrinia* but are absent on the most posterior, just as in large ursids and felids. Situated laterad of the posterior zyg-

Fig. 15. Anterior view of left humerus, *Ysengrinia americana* (probable male, CM 2400), from 8 to 10 miles (~13–16 km) east of the Agate Quarries, ?Arikaree Group, Sioux County, Nebraska, compared with a distal left humerus (probable female, F:AM 25421) of the same species from Morava Ranch Quarry, Upper Harrison beds, Box Butte County, Nebraska. Scale bar, 1 cm.

apophyses, these processes reinforce the zone of spinal flexure at, and posterior to, the anticlinal vertebra, indicating together with the orientation of the zygapophyses that there was a pronounced dorsoventral bending of the vertebral column when running. The lumbar zygapophyses are set close to the midline in *Ysengrinia*, very similar to the zygapophyseal spacing of *Panthera*.

The cervical vertebra (6th) differs from those of both large extant felids and ursids in slightly greater height of the neural arch, but its general form is much like that of *Ursus arctos* of similar size. Although the centrum is proportionately more elongated than that of *U. arctos*, the form, orientation, and surface area of the zygapophyses and details of the neural spine, arch, and transverse processes are configured as in that species.

The atlas vertebra is nearly identical to the atlas of a Siberian tiger (*P. tigris*). These both differ from the atlas of living ursids which fuse the anterior edge of the transverse process with the anterior margin of the vertebra. When fused, the transverse process encloses a foramen that is placed between the transverse foramen and canal (in the process) and the intervertebral foramen at the anterior end of the vertebra, a specialized trait of ursine ursids not seen in *Y. americana*.

The thoracic vertebra is damaged but appears to be the last thoracic anterior to the anticlinal vertebra. It does not differ significantly from this vertebra in either ursids or felids.

A single elongate caudal vertebra indicates the presence of a long tail in *Y. americana*.

SACRUM: A nearly intact sacrum from Harper Quarry (UNSM 44628) is the only known example of this segment of the vertebral column in the genus. It is made up of three vertebrae, the most common number in Carnivora. The *Ysengrinia* sacrum compares well with those of *P. leo* and *P. tigris* which also include three sacral vertebrae. Davis (1964: 112) suggested that the longer sacrum of *Ursus*, in which four to six vertebrae are commonly incorporated, was "associated with increased horizontal thrust on the pelvis .... Extending the sacrum posteriorly increases the attachment area for the multifidus and sacrospinalis muscles. The main action of ... these muscles is to extend the vertebral column when acting on the vertebrae, or to extend the pelvis when acting on the sacrum. These actions are obviously important for spinal fixation .... It seems likely that

Fig. 16. Radius (UNSM 44600, left) and ulna (UNSM 44604, right) of *Ysengrinia americana*, Harper Quarry, Upper Harrison beds, Sioux County, Nebraska. **A,** anterior view of radius, lateral view of ulna; **B,** posterior view of radius, medial view of ulna.

reduction in tail length is a consequence of increased sacral length, although critical data are lacking. If sacral length is increased to provide additional area for the spinal erectors, this area could be provided only at the expense of the basal tail muscles''. The short tails of ursids with long sacra contrast with the very long tails of amphicyonids and species of *Panthera*, which all have short trivertebral sacra.

Fig. 17. Distal radius and proximal ulna of *Y. americana* paratype, F:AM 54147, Upper Harrison beds, 25 Mile District, Goshen County, Wyoming. Scale bar, 1 cm.

INNOMINATE: Two innominates, damaged by scavengers, were found in Harper Quarry, and a more complete innominate occurred at Morava Ranch Quarry (fig. 14C). Those from Harper Quarry are from individuals larger than the Morava Ranch specimen. The innominate is massive, the bone very thick, particularly surrounding the acetabulum. The acetabular diameter for each of the three individuals is 49.0, 47.8, and 45.2 mm (table 4). Despite breakage, the ilium is most similar to the elongate ilium of large living felids. The ischium is also long, not shortened as in some carnivores such as *Ailuropoda*, and the ischial tuberosity for the hamstrings was well-developed but not everted as in living ursids. The most evident similarity to the ursid innominate is the widened ventral surface of the ilium anteromedial to the rectus femoris tuberosity for the origin of the iliacus muscle. This probably reflects a very large iliopsoas muscle complex for flexion of the thigh in this heavily muscled amphicyonid. However, the overall form of the *Y. americana* innominate most closely parallels this bone in large living felids. In *P. leo* and *P. tigris* the ilium and ischium are more anteroposteriorly aligned than in living ursids in which a flared ilium and short, everted ischium are typical.

BACULUM: A large baculum at Harper Quarry measured 24 cm in length (fig. 14C), lacking only the tip of about 1 cm. Although not associated with other elements, it demonstrates that males are present in the bonebed, and supports the inference that skeletal dimorphism is sexual. The *Y. americana* baculum is nearly perfectly straight for its proximal 18 cm, then curves downward for its distal 5 cm, hence it differs from the smaller but entirely straight baculum of *Ursus* (a Kodiak Island *U. arctos* baculum measures only 15.2 cm in length). A weak urethral grove in the ventral surface of the bone begins about

Fig. 18. *Ysengrinia americana*: **A,** metacarpal 5 (UNSM 44611, female); **B,** metacarpal 5 (UNSM 44615, male); **C,** metacarpal 2 (UNSM 44619); **D,** metacarpal 4 (UNSM 44617); **E,** scapholunar (UNSM 44609); **F,** pisiform (USNM 186993). Metacarpals and scapholunar are from Harper Quarry, Sioux County, Nebraska. Pisiform is from Lay Ranch beds, west of Spoon Butte, Goshen County, Wyoming.

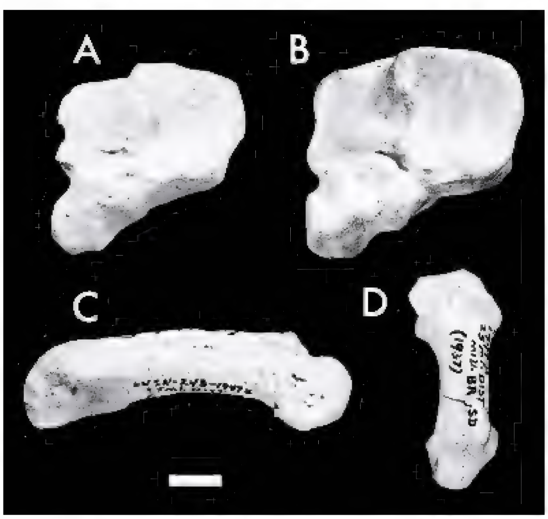


Fig. 19. Scapholunars and metacarpals of *Y. americana*: **A,** scapholunar, F:AM 54147, paratype; **B,** scapholunar, UNSM 44610, Harper Quarry; **C,** metacarpal 5, and **D,** metacarpal 1, both from F:AM 54147, paratype. Scale bar, 1 cm.

6 cm from the proximal end and continues to the distal tip; however, the terminal 4–5 cm of the groove deepens and widens, opening at the distal end of the baculum which flares to form a bifurcated tip. In large living felids the baculum is quite short (~1 cm) and small.

FEMUR: There are three complete femora of *Y. americana*, one from the Lay Ranch beds at Spoon Butte, two from Harper Quarry. The two complete bones from Harper Quarry differ in size, one large and robust (UNSM 44624), the other a more gracile femur from a much smaller individual (UNSM 44690). These are probably male and female: the diameter of the femoral head (41.1 and 40.0 mm, respectively) is nearly equal, but the width of the proximal femoral neck (69.8 vs. 61.0 mm, measured at the level of the lesser trochanter) and the midshaft width of the diaphysis (43.0 vs. 35.3 mm) differ appreciably. The femur from Spoon Butte is an

TABLE 4

Comparative Measurements (in mm) of the Innominate in North American Early Miocene Amphicyonids and Some Living Felids, Ursids, Hyaenids, and Canids

	A-P diameter of acetabulum[a]	Center of acetabulum to anterior border of ilium	Center of acetabulum to posterior border of ischium	Museum number	Sex
AMPHICYONIDAE					
Daphoenodon superbus	31.1	(122)[b]	115	UNSM 70-85	
D. superbus	28	(120)	—	CM 1589	
Ysengrinia americana	47.8	(175)	(120)	UNSM 44626	
Y. americana	49.0	—	—	UNSM 44627	
Y. americana	45.2	(170)	116	ACM 9761	
FELIDAE					
Panthera leo	44.0	170	120	AM 85140	M
P. leo	40.2	172	116	AM 85142	M
P. leo	44.3	186	131	AM 85143	M
P. leo	41.1	179	119	AM 85144	M
P. leo	40.4	162	124	AM 85145	F
P. leo	37.9	157	117	AM 85147	F
P. leo	46.1	184	132	AM 85149	M
P. leo	45.2	168	121	AM 36814	M
P. leo	41.2	166	125	AM 119477	F
P. leo	49.8	190	(150)	UNSM 14278	M
Panthera tigris (Sumatra)	35.3	158	110	UNSM 14602	?
P. tigris(Sumatra)	31.7	151	105	AM 14030	M
P. tigris(zoo)	40.1	162	123	AM 14032	M
P. tigris(India)	40.5	166	122	AM 217100	F
P. tigris(Siberia)	48.2	194	145	AM 85404	M
P. tigris(Siberia)	42.6	176	124	AM 85405	F
P. tigris(Siberia)	47.8	185	140	UNSM 16656	M
Panthera concolor	28.7	137	100	UNSM 19688	M
Panthera onca	27.3	109	82	UNSM 16919	F
URSIDAE					
Ursus americanus	35.2	125	(75)	UNSM 18705	?
U. americanus	35.7	136	83	UNSM 3253	F
U. americanus	37.0	147	88	UNSM 16986	F
U. americanus	38.5	134	92	AM 128521	?
U. americanus	43.2	165	119	AM 24157	?
Helarctos malayanus	27.2	107	66	UNSM 13875	F
Helarctos malayanus	32.4	116	87	AM 35364	F
Tremarctos ornatus	40.0	168	102	AM 217862	?
Ursus arctos	50.2	184	120	AM 70330	F
U. arctos	45.2	169	114	AM 128463	F
U. arctos	59.6	230	160	UNSM 19565	?
U. arctos(Kodiak)	63.5	235	170	UNSM 17888	M
U. arctos(Kodiak)	60.7	247	172	AM 70163	M
Thalarctos maritimus	68.5	250	175	UNSM 16938	M
T. maritimus	65.3	234	158	AM 75244	?
HYAENIDAE					
Crocuta crocuta	33.8	123	75	UNSM 16470	M
C. crocuta	32.3	134	76	UNSM 16471	F
CANIDAE					
Canis lupus	30.8	124	81	UNSM 17459	F
C. lupus	30.3	119	80	UNSM 17458	F
C. lupus	28.0	114	74	UNSM 15596	F
C. lupus	27.4	113	74	UNSM 12641	F
C. lupus	26.6	113	72	UNSM 3462	?

[a] A-P = anterior-posterior.

[b] ( ) Indicates estimated measurement.

even larger individual, probably a male (USNM 186993, diameter, femoral head, 46.2 mm; width of proximal femoral neck, 71.0 mm; diaphyseal width, 45.4 mm) , and is associated with a tibia (fig. 20), providing the only known femorotibial index for a single individual of *Y. americana* (79.8, table 2).

The femur is columnar and straight, its diaphysis of nearly equal diameter throughout its length, reflecting the body weight supported by the hindlimb and its muscular power. It shares some similarities with femora of large living ursids, but compares most closely with those of living felids. It differs from femora of extant ursids in the following features: (1) in *Ursus arctos*, *U. americanus*, and *T. maritimus* the femoral diaphysis is relatively slender and more elongate than in *Ysengrinia*—the bone tapers to a gracile midshaft diaphysis, widening at the distal end, even in the largest living ursids; (2) the distal femoral condyles in *Ursus* are low and broad, whereas *Ysengrinia* shares the taller, narrower distal condyles of *Panthera leo*—the intercondylar depression or groove is deep and symmetric in *Ysengrinia*, shallow to deep and asymmetric in *Ursus*; (3) the deep pits or scars for the lateral and medial heads of the gastrocnemius situated on the dorsal margin of the lateral and medial femoral condyles face posteriorly in *Ursus* but have a shallower and more lateral orientation in *Ysengrinia* and large living felids; (4) the distal end of the femur in living bears is asymmetric, due to the more expanded medial epicondylar region—in large living felids and *Ysengrinia* the distal end of the femur is symmetric. The femur of *Y. americana* compares particularly well with the femora of *P. leo* and *P. tigris* but is somewhat more robust in large males.

TIBIA: The tibia is the best represented limb bone of the species: there are four from Harper Quarry and one associated with the femur from Spoon Butte (USNM 186993). Although the Spoon Butte femur is larger than the femora from Harper Quarry, the tibia (fig. 20) associated with this femur is shorter and somewhat more robust than any of the Harper Quarry tibiae. The general form of the tibia is most similar to those of large living felids; the felid tibia differs primarily in a more elongate diaphysis. Living large ursine bears and *Y. americana* share a particularly robust tibia. However, the principal distinction between living ursids on the one hand, and *Y. americana* and large felids on the other, involves the distal articular surface of the tibia: the wider and shorter astragalus of *Ursus* corresponds to a shallower, wider articulation surface on the distal tibia, whereas this surface is narrower and more deeply grooved in *Y. americana*, *P. leo*, and *P. tigris*. These latter three species also show a more fore-aft alignment of the trochlear grooves on the distal tibia for reception of the astragalus than is found in living ursids. In addition, there is a tight registration between distal tibia and astragalus in the large felids and *Y. americana*, but the fit is looser, less congruent, in large ursids in which intervening soft tissue must compensate for the slack registration in the living animal.

If we calculate the femorotibial index for the hindlimbs from Harper Quarry (using the largest femur and tibia) and from Spoon Butte, the range of values (79.8–81.6) for *Y. americana* falls between living ursids (67.9–75.9) and the large living species of *Panthera* (*P. leo*, 83.7–89.3; *P. tigris*, 83.4–87.6), indicating that, relative to the hindlimb proportions of living bears, the *Y. americana* tibia is elongated, approaching the felid ratios (table 2).

TARSALS: An astragalus (fig. 21) is associated with the tibia of the Spoon Butte *Ysengrinia*. Three calcanea and an astragalus come from Harper Quarry, and a somewhat larger calcaneum from American Museum–Cook Quarry. A right ectocuneiform from Morava Ranch Quarry (fig. 21) is the only other tarsal element in these collections.

The astragali of living bears and *Ysengrinia* are markedly different. In plantigrade *Ursus* the astragalar trochlea is broadened and the neck is shortened significantly relative to *Y. americana*. The *Ysengrinia* astragalus resembles that of large living felids in which a narrow trochlea with well-defined trochlear ridges is positioned above a longer neck. In *Y. americana*, however, the neck is not quite as elongated as in felids and is not as narrow, and the sustentacular facet is not restricted to the more dorsal part of the neck as it is in digitigrade cats. In living *Ursus* the area oc-

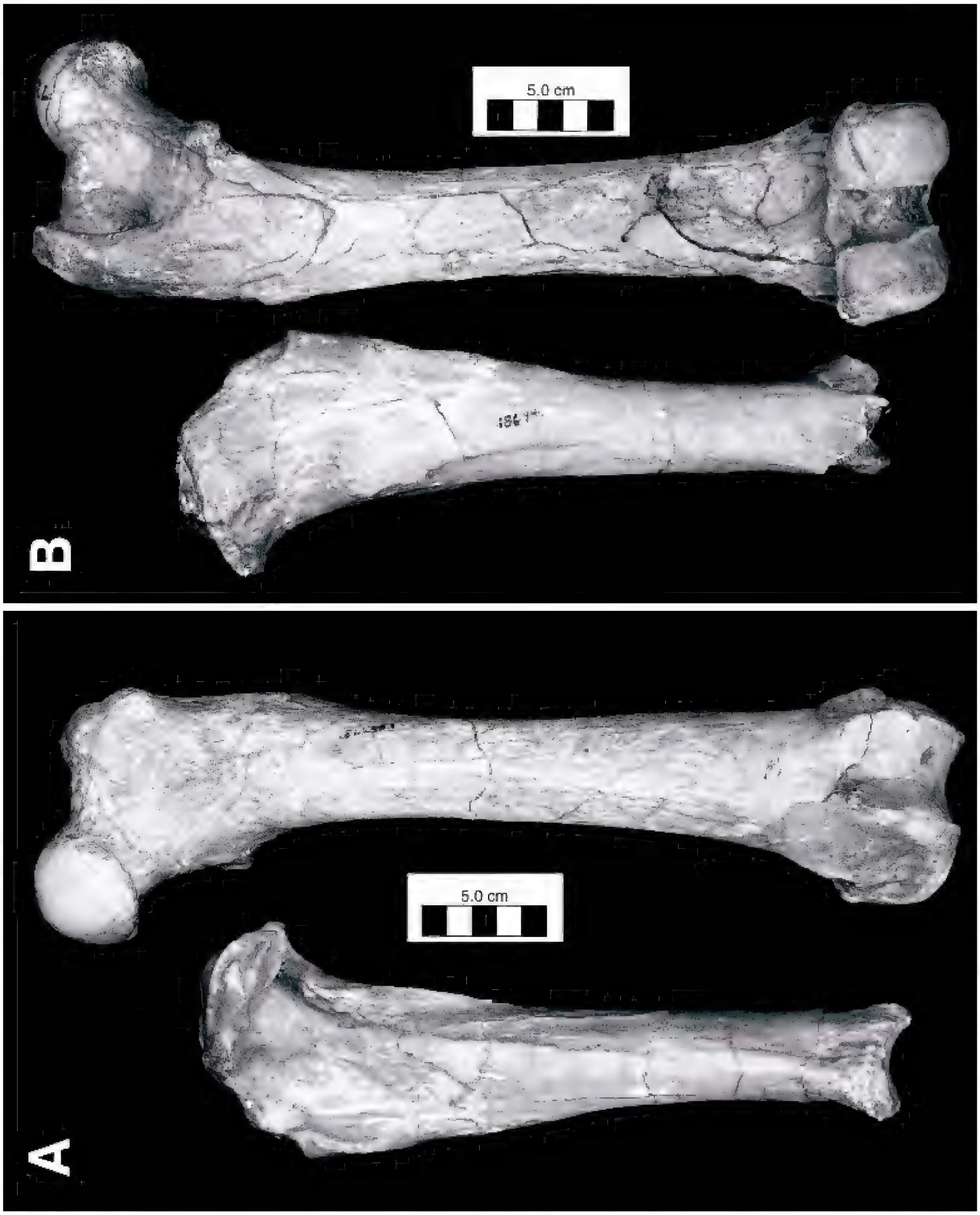


Fig. 20. Associated right femur and tibia, *Ysengrinia americana* (USNM 186993), Lay Ranch beds, west of Spoon Butte, Goshen County, Wyoming: **A,** tibia, lateral view; femur, anterior view; **B,** tibia, medial view; femur, posterior view.

Fig. 21. *Ysengrinia americana*: **A,** ectocuneiform (ACM 9390); **B,** carpal cuneiform (USNM 186993); **C,** metatarsal 5 (UNSM 44634, male); **D,** metatarsal 5 (UNSM 44633, female); **E,** astragalus (UNSM 44630, female); **F,** astragalus (USNM 186993, male).

cupied by the sustentacular facet extends distally farther along the neck, an anatomical trait typical of ursid plantigrady. The *Y. americana* astragalus lacks the astragalar foramen which is often lost in carnivorans that approach or have attained digitigrady in the hindfoot (this foramen is occasionally present in digitigrade felids, e.g., UNSM 16656, *P. tigris*, Siberian tiger).

The three calcanea from Harper Quarry are of about the same size and can articulate appropriately with the astragalus from Harper Quarry (fig. 21E). This astragalus is ~7% smaller than the large astragalus from Spoon Butte (fig. 21F), a measure of dimorphism in this species. The calcanea are not anatomically specialized for a fully digitigrade stance: (1) the distal calcaneum below the sustentaculum is not as short as in living ursids but is not as elongated as in large digitigrade *Panthera*; (2) the posterior surface of the sustentaculum is not as deeply grooved for a flexor tendon of the digits (flexor hallucis longus) as in digitigrade felids and canids in which the distal calcaneum is mediolaterally narrower; (3) although the medial facet remains separate from the anterior facet in three out of four calcanea, they are slightly conjoined in the largest individual (CM 2211). In large plantigrade ursids (*U. arctos*, *T. maritimus*) the medial and anterior articular facets of the calcaneum are conjoined (Stains, 1973), presumably due to body weight transmitted downward through the superposed astragalus. The fusion of these calcaneal facets does not occur in digitigrade felids.

Other features of calcaneum and astragalus are more typical of digitigrade carnivores: (1) the general form of these bones closely approaches that of *P. tigris* and *P. leo*, but differs primarily in being more robust, massive; (2) the relatively narrow parallel-sided and grooved trochlea of the astragalus and its tight registration and arc of rotation on the distal tibia are as in the large digitigrade felids; (3) the sustentacular facet of the astragalus remains confined largely or entirely to the neck of the astragalus as in felids and does not continue dorsad to the summit of the trochlea as in large ursids; (4) the calcaneum of plantigrade *Ursus arctos* is dis-

tally broader and has a proportionately larger sustentaculum relative to *Ysengrinia*, presumably due to its greater weight-bearing role; (5) the peroneal tubercle of the distal calcaneum, involved in eversion of the plantigrade hindfoot, is prominently developed in large living ursids but remains only of modest size in large digitigrade felids and *Y. americana*.

Ysengrinia americana does not show the specializations of calcaneum and astragalus for plantigrady found in living ursids, but neither has it achieved the fully digitigrade calcaneum-astragalus of large living felids and canids. In *Y. americana* the entire sole of the hindfoot may have occasionally contacted the substrate when standing at rest, but when in motion adopted a more elevated "subdigitigrade" stance. This is suggested by measurements of the arc of rotation of the astragalus on the distal tibia (table 5; see Wang, 1993). These data were used to estimate the amount of plantar and dorsiflexion of the hindfoot on the lower limb. The extreme plantar flexion observed in digitigrade canids (73–76°) is not achieved in most living plantigrade ursids (37–47°). *Y. americana* (47–50°) shows a somewhat greater degree of plantar flexion than seen in these ursids. The maximum amount of rotation of the astragalus on the tibia, measured in degrees of arc, occurs in digitigrade canids and felids (80–96°); ursids and *Y. americana* show a lower range of values (54–66°), with the exception of the carnivorous polar bear (74°). However, a digitigrade stance is not necessarily accompanied by high values for plantar flexion, as shown by brown and spotted hyenas (table 5) relative to canids and felids.

The ectocuneiform (fig. 21), known only from Morava Ranch Quarry, differs considerably from the low, tabular ectocuneiform of *Ursus*, resembling much more closely this bone in *Panthera leo* and *P. tigris*. Moreover, the form of the ectocuneiform and its cuboid facets allows a reliable estimation of the form of the cuboid. The lateral face of the *Y. americana* ectocuneiform shows three separate facets for articulation with the cuboid: the largest is the nearly quadrate dorsal facet which is typical of amphicyonids; there are also smaller anterior and posterior ventral facets. This differs from the smaller dorsal facet in large species of *Panthera*, which is prolonged ventrad as a narrow linear crest. In *Ursus arctos* the dorsal facet is much larger and rectangular, extending nearly to the rear of the bone; its form in these bears is a specialization of the plantigrade tarsus. The convex surface of the dorsal facet in large *Ursus* indicates a greater degree of movement between the cuboid and ectocuneiform than in *P. tigris*, *P. leo*, and *Y. americana* in which a more planar surface suggests more limited motion between these bones. The two ventral facets are present in large living ursids, but the dorsal facet is conjoined with the anterior ventral facet, forming a broad surface of articulation with the cuboid, a feature not evident in large felids. In *Y. americana* the anteroventral facet is much smaller, and a posteroventral facet is added in the beardog which is absent in *P. tigris*. The posterior process of the ectocuneiform is prominently developed in *Ysengrinia* and the great cats but is very reduced in *Ursus*. The medial face of the ectocuneiform in large living felids, ursids, and *Y. americana* is similar in having an elongate dorsal facet for the mesocuneiform and two separate anterior and posterior ventral facets for the head of metatarsal 2. The ventral surface of the ectocuneiform for articulation with the head of metatarsal 3 most resembles that in *P. tigris*.

METATARSALS (fig. 14B): The form of the proximal heads of the metatarsals and the anatomical detail of the articular facets are developed as in large *Ursus* (*U. arctos*). Differences are: (1) a somewhat closer registration of the proximal articulations in *Ursus*; (2) a reduction in size of metatarsal 1 in *Y. americana* relative to *Ursus*; (3) a paraxonic hindfoot in *Ysengrinia*, similar to large living *Panthera* in which metatarsals 3–4 are the longest and of about equal length (metatarsals 2 and 5 are shorter), whereas in *Ursus* the hindfoot is not paraxonic, the longest metatarsals are 5–4, diminishing progressively in length through metatarsals 3–2–1. Dimorphism in *Ysengrinia* (fig. 21C, D) is demonstrated by 2 fifth metatarsals of equal length from Harper Quarry, one robust (UNSM 44634), the other gracile (UNSM 44633).

The orientation and relative lengths of the metacarpals and metatarsals in large living

TABLE 5

Comparative Measurements (in degrees of arc) of the Rotation of Astragalus on Distal Tibia in the Early Miocene Amphicyonid *Ysengrinia* and in Living Ursids, Felids, Canids, and Hyaenids

	Plantar flexion[a]	Dorsi-flexion[a]	Degrees of arc[b]	Museum number
Amphicyonidae				
Daphoenodon superbus	57	−22	79	CM 1589
Ysengrinia americana	47	−14	61	USNM 186993
Y. americana	50	−14	64	UNSM 44620, 44630
Ursidae				
Ursus americanus	47	−19	66	UNSM 15112
U. americanus	42	−23	65	UNSM 16986
Helarctos malayanus	37	−23	60	UNSM 13875
Ursus arctos (Kodiak)	40	−14	54	UNSM 17888
Thalarctos maritimus	60	−14	74	UNSM 16938
Felidae				
Panthera tigris (Siberia)	61	−31	92	UNSM 16656
P. tigris (Sumatra)	62	−24	86	UNSM 14343
P. tigris (Sumatra)	54	−26	80	UNSM 14602
Canidae				
Canis lupus	73	−22	95	UNSM 17458
C. latrans	76	−20	96	UNSM 14166
Hyaenidae				
Crocuta crocuta	50	−22	72	UNSM 16471
C. crocuta	53	−18	71	UNSM 16470
Hyaena brunnea	50	−20	70	UNSM 15506

[a] The astragalus is articulated with the distal tibia so that the long axis of the astragalus is horizontal and at a right angle to the long axis of the tibia. The extent of plantar flexion is determined by rotating the astragalus downward from the horizontal until a limit is indicated by bony stops or lineations on the dorsal trochlea. The degree of plantar flexion is the vertical angle (+) between the horizontal and the downward limit of astragalar rotation. The extent of dorsiflexion is similarly measured as the vertical angle (−) between the same horizontal and the limit of upward rotation of the astragalus on the tibia, indicated by the point at which the apposed articular surfaces of the distal tibia and distal trochlea of the astragalus coincide at their limit.

[b] The degrees of arc measures the total amount of rotation of the hindfoot on the tibia (lower leg) when moved from the fully dorsiflexed to fully plantar flexed position. It is the angle in degrees between extreme dorsiflexion and extreme plantar flexion.

ursids (Ursinae) reflect the turning-in of their feet, a specialization of ursine bears not found in other Carnivora. This is interpreted as a secondary modification of the plantigrade stance of early Tertiary carnivorans.

SUMMARY: The nearly complete representation of the postcranial skeleton of *Y. americana* provides the first definitive evidence of its size, stance, and gait. The robust, massive limb elements and stout vertebral column indicate a large, heavy, muscular carnivore. At first the postcranial skeleton of *Ysengrinia americana* appears to be a composite of features found in both large living felids and ursids, integrated with features exclusive to amphicyonids (table 6). Earlier studies of amphicyonid postcranial skeletons remarked on resemblances to felids (Hatcher, 1902; Hough, 1948) and to ursids (Ginsburg, 1961). Such skeletal correspondences have been interpreted by some workers as evidence of direct relationship to these groups. However, comparisons with postcrania of a broad spectrum of fossil and extant Carnivora suggest that many of the resemblances of *Y. americana* to large living ursids in fact reflect their shared arctoid ancestry. On the other hand, the "felid" traits of this beardog (table 6: scapholunar, lumbar vertebral column, sacrum, and tail, pelvis, hindlimb elements) are regarded here as primitive carnivoran postcranial features scaled to large size, or, with regard to fore- and hindlimb proportions, as ecological adaptations of this particular species. In fact these "felid" traits are almost certainly early arctoid skeletal fea-

TABLE 6
Summary Comparison of Postcranial Traits of the Early Miocene Amphicyonid *Ysengrinia americana* Relative to Postcrania of Large Living Ursids and Felids

	Ysengrinia	Arctoid (="ursid")	"Felid"
FORELIMB			
Scapula	x	x	
Humerus	x	x	
Radius-Ulna	x	x	
Humeroradial index	x		x
Scapholunar	x		x
Unciform	x	x	
Pisiform	x	x	
Metacarpals	x	x	
Phalanges	x	x	
AXIAL SKELETON			
Vertebrae	x	x	x
Sacrum	x		x
HINDLIMB			
Innominate	x		x
Baculum	x	x	
Femur	x		x
Tibia	x		x
Femorotibial index	x		x
Astragalus	x		x
Calcaneum	x	x	
Ectocuneiform	x		x
Metatarsals	x	x	

An "x" indicates that characteristic anatomical features of the postcranial element(s) are comparable between or among the groups so designated.

tures that were not overprinted by postcranial specializations such as those of ursine bears. The undisputed anatomical specializations of the living ursine bears, such as their unique dentition, foot anatomy, and derived plantigrade gait, are not seen in amphicyonids.

As various species of ursids and amphicyonids independently attained large body size, arctoid postcranial characters were expressed as slightly divergent morphs, particularly evident in the fore- and hindfeet. For example, living bears achieved their specialized form of plantigrady and the amphicyonids a subdigitigrade stance, but their common ancestry remains evident in anatomical details of the basicranium and various postcrania. The postcranial features of the *Ysengrinia* skeleton that proclaim an arctoid origin are found in the scapula, humerus, baculum, proximal metapodials, and phalanges. The amphicyonid skeleton indicates that the family evolved independently of both ursids and felids during the Cenozoic, yet paralleled the large species of these groups in a number of adaptive traits related to the life mode of large terrestrial carnivorans.

Ysengrinia americana fossils are consistently found in waterhole and fluvial settings, suggesting that the animal was a frequent visitor to these places, probably preying on and scavenging mammals congregating at such water sources. The postcranial skeleton indicates that *Ysengrinia* was an ambush predator that relied on a burst of speed to overtake its prey, and on its grasping, powerful forelimbs and huge canines to dispatch these animals.

BASICRANIAL ANATOMY

Well-preserved basicrania of early Miocene amphicyonids are almost entirely represented by North American specimens, with a few (<10) from western Europe; none are known from Asia or Africa. Early Miocene amphicyonids retain plesiomorphic arctoid basicrania in which the middle ear cavity has not invaded surrounding skull bones, and the auditory bulla is not greatly enlarged. In carnivorans in which the auditory bulla has expanded to accommodate an increased middle ear volume, the bulla encroaches on adjacent bones, modifying the form of the basicranium. This does not occur in these amphicyonids which are distinguished by a broad basicranial axis (wide basioccipital and basisphenoid) and a mastoid-occipital region unmodified by expansion of the auditory bulla.

The paratype skull of *Y. americana* provides information on the auditory bulla and some surrounding features of the basicranium for the first time (fig. 22).

AUDITORY BULLA: The auditory bulla in many species must have been only loosely attached to the basicranium because it is often missing in otherwise intact crania. The early Miocene skulls from North America that retain an intact or only slightly distorted auditory bulla are few, but can be divided into four types: (1) species referred or closely related to *Daphoenodon* all display a uniform morphology of the bulla similar to that of the

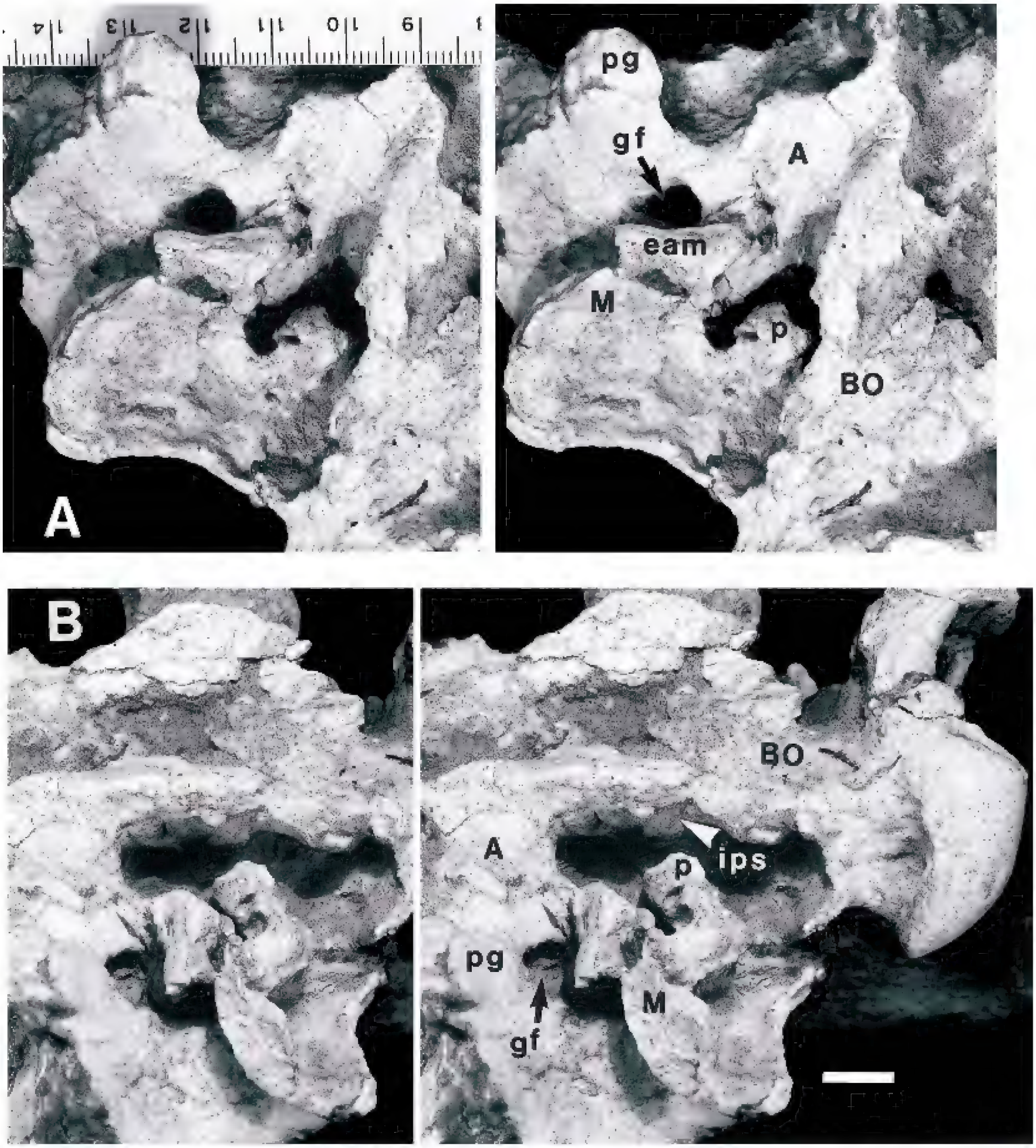


Fig. 22. Basicranium of *Ysengrinia americana*, paratype (F:AM 54147): **A,** ventral view; **B,** lateral oblique view. Metric scale in A; scale bar in B is 1 cm.

D. superbus holotype skull (CM 1589); (2) although known only from the paratype skull of *Y. americana* (F:AM 54147), the poorly preserved bulla of North American *Ysengrinia* evidently differed from the bulla of *Daphoenodon* in having a longer bony external meatal tube and in being more deeply recessed in the auditory region (no basicrania of *Ysengrinia* are known from the Old World); (3) the relatively unspecialized bullae of *Daphoenodon* and *Ysengrinia* differ from the bulla of early Miocene North American *Amphicyon* (F:AM 25400) where the middle ear cavity invades the bony floor of

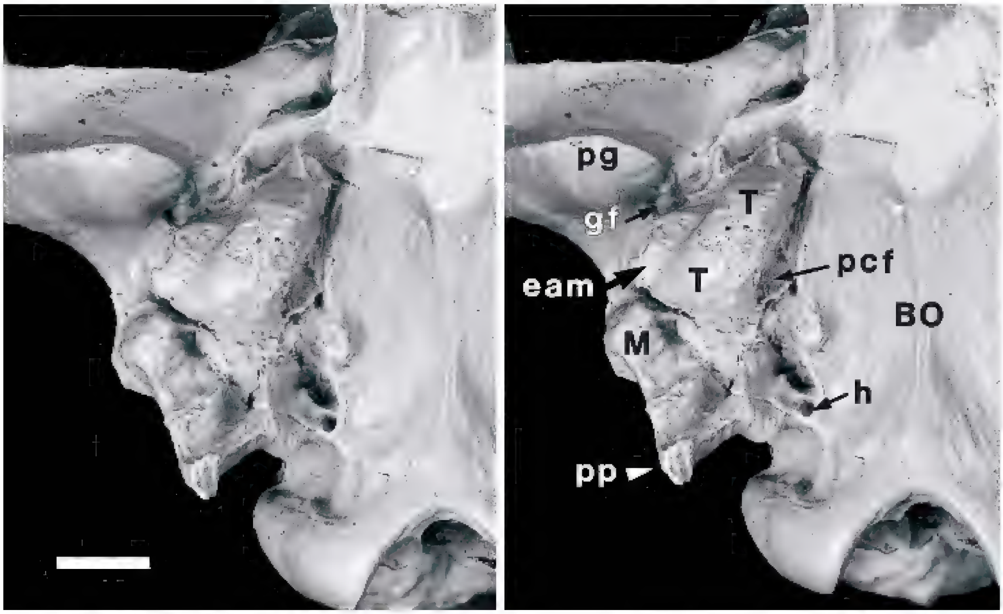


Fig. 23. Basicranium of *Daphoenodon superbus*, holotype (CM 1589), Upper Harrison Beds, Carnegie Quarry 3, Agate Fossil Beds National Monument, Sioux County, Nebraska. Stereophotographs of high-resolution cast. Scale bar, 1 cm.

an enlarged external auditory meatus, thereby increasing middle ear volume (Hunt, in press); (4) only three temnocyonine skulls retain an auditory bulla, each a different species; two of these skulls preserve a rudimentary crescentic ectotympanic without evident entotympanic contributions; the skull of a third species retains a more evolved ectotympanic bulla that probably includes small entotympanic elements.

In *Daphoenodon superbus* (CM 1589), a simple, capsular bulla encloses the petrosal (figs. 23, 24B). The bulla is somewhat ventrally inflated in its medial half and has a short bony external auditory meatus. An osseous tube for the internal carotid artery runs within its medial wall; a large posterior carotid foramen at the posteromedial corner of the bulla marks the entrance of the artery. The osseous bulla does not extend behind a transverse line drawn through the mastoid processes, demonstrating that there was no posterior expansion of the bulla. Much of the posterior auditory region remained uncovered. However, the bulla does extend into the anteromedial corner of the auditory region, ~4–5 mm anterior to the level of the postglenoid processes. Compared to the bullae of living arctoid carnivorans, the bulla of *D. superbus* is extremely rudimentary. The bulla is thin-walled, weakly attached to the skull, lacking any posterior expansion. It is formed mostly or entirely by an ectotympanic element, and thus differs from the thick-walled, posteriorly and ventrally inflated, ankylosed bullae of many living arctoids that are formed by both ectotympanic and entotympanic elements (Hunt, 1974). The presence of an entotympanic contribution in *Daphoenodon* remains uncertain, but if present, it was confined to the posteromedial margin of the bulla and was very small.

In *Y. americana* (figs. 22, 24A, F:AM 54147), the weathered, partly decomposed basicranium retains remnants of the bullae, basicranial axis, and petrosals. Basioccipital width, measured at the level of the petrosal promontoria, is ~35–38 mm. Its lateral margin contains the embayment for the expanded inferior petrosal venous sinus common to amphicyonids. The petrosals are deeply inset in the auditory region, are small relative to the size of the skull, and lie medial to well-developed mastoid processes, as in North American *Amphicyon*. In *Daphoenodon su-*

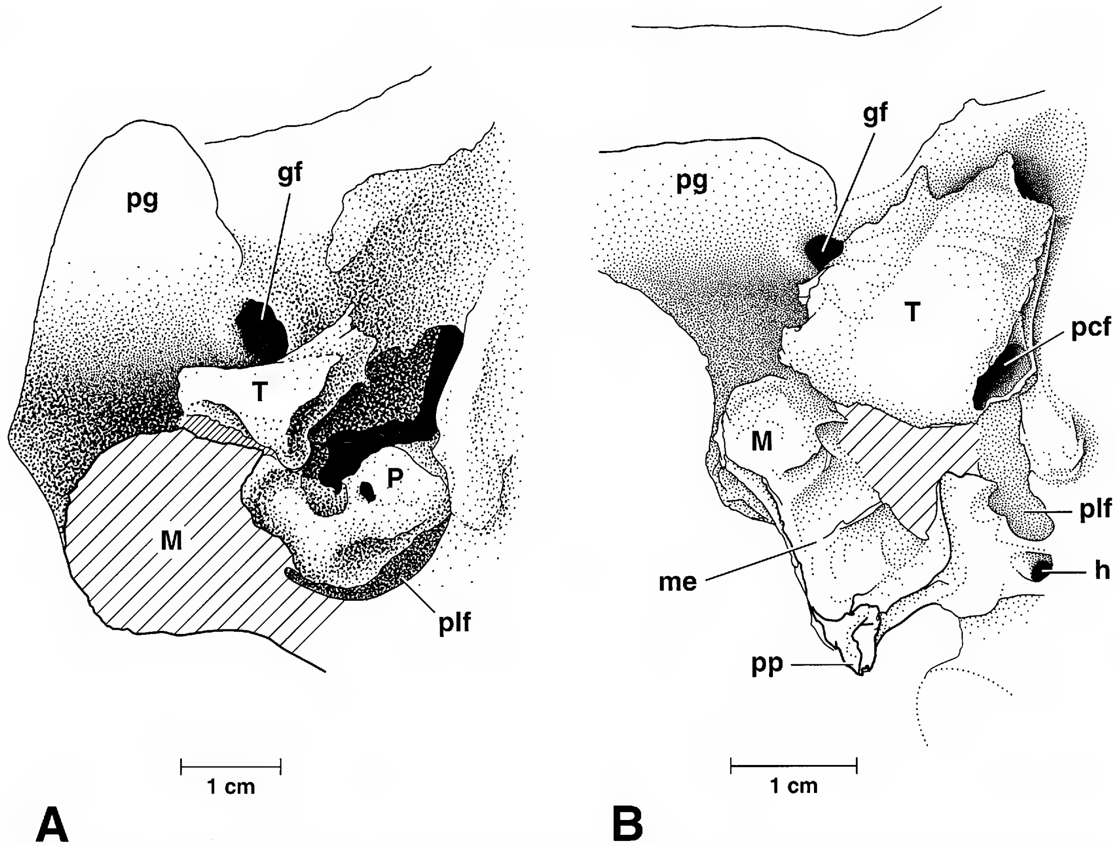


Fig. 24. **A,** Auditory region of *Ysengrinia americana*, paratype (F:AM 54147, fig. 22), Upper Harrison beds, 25 Mile District of Falkenbach, Goshen County, Wyoming; **B,** auditory region of *Daphoenodon superbus*, holotype (CM 1589, fig. 23), Upper Harrison Beds, Carnegie Quarry 3, Agate Fossil Beds National Monument, Sioux County, Nebraska. In *Ysengrinia* the auditory bulla medial to the bony external auditory meatus has been lost from the skull but is presumed to have been a low flask-shaped chamber with a bony tube within its medial wall for the internal carotid artery, similar to the tube (pcf) in *Daphoenodon*.

perbus the petrosals are not deeply inset in the skull.

The bulla remnants in *Y. americana* consist of a small part of the anterior wall and the bony external auditory meatal tube which was somewhat elongated. The middle ear cavity did not extend into the floor of the bony meatus as occurs in *Amphicyon*. Despite the absence of much of the bulla, the orientation of the remaining bone suggests the bulla was little if at all inflated, and was not posteriorly extended. It probably reached only to the posterior margin of the petrosal as in *Amphicyon*. The width of the capsular part of the bulla internal to the bony meatus was no greater than 10–11 mm. There is no evidence of any extension of the middle ear cavity into surrounding basicranial bones. One can conclude that the bulla of *Ysengrinia* was a simple, rudimentary bony ectotympanic capsule, covering little more than the petrosal itself. It lacked inflation, ankylosis to surrounding bones, or other specializations seen in various living arctoid carnivorans.

In the Old World the only early Miocene amphicyonid skull that preserves an intact auditory bulla is the Jourdan cranium of *Cynelos lemanensis* from St.-Gérand, France (Hunt, 1977: pl. 1). Its form differs somewhat from that of *Daphoenodon* and *Ysengrinia* but it also was a simple capsular structure with a short bony meatal tube. The me-

dial part of the bulla probably was slightly inflated as in *D. superbus*. The bulla is situated almost entirely forward of a transverse line through the mastoid processes in the same manner as in *Ysengrinia* and *Daphoenodon*, and there is no extension of the bulla into the posterior auditory region. As in other amphicyonids, the bulla is formed primarily by the ectotympanic. Of interest is whether one or more entotympanic elements were added to the periphery of the ectotympanic as occurs in living ursids (Hunt, 1974). This could be determined by observing the ontogenetic elements making up the bulla of young individuals, but no juveniles with intact bullae are known as fossils. Because the *Cynelos* bulla is similar in form to that of living *Ursus americanus* in which small entotympanics (E_1, E_2) are attached to the inner margin of the ectotympanic (Hunt, 1974: pl. 4), it is possible that rudimentary entotympanics contribute to the bullae of *Cynelos lemanensis* (Hunt, 1977; Ginsburg, 1977) and to a species of temnocyonine from the upper John Day beds of Oregon (Fingerhut et al., 1993).

PETROSAL: There are no evident anatomical specializations of the petrosal in early Miocene North American amphicyonids: the low promontorium and adjoining tegmen are similar in form and proportions. Based on the distribution and shape of fossae and the facial canal on the tegmen's surface, the auditory ossicles, auditory muscles, and course of the facial nerve were morphologically uniform in these carnivorans. The anatomical pattern of the tegmen is very similar to that of living ursids (e.g., *Ursus americanus*).

Although damaged, the petrosal of *Y. americana* conforms to the amphicyonid pattern.

DENTITION AND FEEDING

The dental formula of 3-1-4-3 in upper and lower jaws is consistent for nearly all species of North American amphicyonids except the temnocyonines, which have lost M3. The migrant amphicyonines that enter North America from Eurasia in the early Miocene all retain the full complement of molars (M1–3/m1–3). The paratype cranium of *Y. americana* lacks the maxilla posterior to M2, so it is uncertain if M3 was retained in this individual, but since the holotype palate retains this tooth it probably was present in the species, albeit reduced and likely nonfunctional. However, it is in the state of the premolars that the Old World migrants differ from the New World endemics. North American daphoenine and temnocyonine amphicyonids retain well-developed premolar batteries in contrast to the migrant amphicyonines *Ysengrinia*, *Cynelos*, and *Amphicyon* that reduce the size of their anterior premolars (P1–3 and p1–3), occasionally entirely losing p2 (fig. 9).

Occlusion of the upper and lower toothrows in many species of carnivorans involves close registration of the carnassials and canines. However, the carnassial teeth are not tightly registered when the mandibles are in centric occlusion. As the jaws are brought together, interlocking of the canines (autocclusal mechanism of Mellett, 1984) guides the approximation of the carnassial blades. In many carnivorans with sectorial carnassials, registration of the chewing mandible with the corresponding upper toothrow involves a lateral shift of the chewing-side mandible as closure takes place. Precise registration of these teeth is effected by neuromuscular control and aided by a mobile mandibular symphysis (e.g., in canids, Scapino, 1965). However, in some other carnivores (the creodonts *Hyaenodon*, *Patriofelis*) with shearing carnassials, the mandibular symphysis can be fused, hence immobile. When this occurs, the chewing mandible cannot shift outward independently of the passive mandible, thereby hindering precise occlusion of the carnassial teeth as the individual grows older and the teeth wear (Mellett, 1977). To compensate, the upper carnassial of these creodonts rotates inward during the life of the animal to maintain contact with the lower shearing tooth.

With the exception of the presence of M3, the teeth of amphicyonids are broadly comparable in form to those of living canids, so much so that they were classified with the Canidae by paleontologists in the first half of the 20th century (e.g., Simpson, 1945). In addition to the similarity in form and number of teeth, the anatomical topography of the mandibular symphysis and temporomandib-

ular joints of North American amphicyonids also corresponds to Scapino's (1965) description of these features in living canids. As in canids, the symphysis of amphicyonids remains unfused, with the exception of some very old adults. Analysis of the amphicyonid feeding mechanism suggests that initiation of the bite was preceded by the autocclusal contact of the canines, followed by precise neuromuscular control of carnassial registration by the jaw muscles. As the jaws came together, the edges of the carnassials were brought into tight registration by a slight lateral adjustment of the chewing mandible, paralleling the mechanism described in a living canid by Scapino (1965). As an individual progressively aged, the molars and carnassials eventually developed subhorizontal to flat wear surfaces in both canids and amphicyonids. In old age, a precise occlusion was no longer possible or necessary because the shearing blades were worn away, leaving only broad grinding surfaces. At this point, some aged beardogs fused the mandibular symphysis and employed a jaw mechanism similar to the crushing occlusion found in living ursine bears.

It is possible to accurately describe dental occlusion and tooth wear in several North American Neogene amphicyonids. Although a range of ontogenetic stages is lacking for *Ysengrinia*, the association of cranium and mandible in the *Y. americana* paratype, a mature adult, can be used to examine how its teeth functioned during its lifetime. As an individual of *Y. americana* aged, its teeth developed the greatest degree of wear in two areas of the dentition: the canines/incisors and the carnassial/molar group (figs. 6B, 7, 9B). Incisors were gradually blunted by wear over time, yielding flat-surfaced pegs. Premolars were not heavily worn even in old individuals, in which wear was limited to the tip of the principal cusp on each tooth (however, on p4 both the principal and posterior accessory cusps are eventually worn flat). The degree of wear increases as one proceeds backward in the toothrow, culminating in heavily worn carnassials and molars; thus, it is evident that food taken into the mouth is transfered to the rear where the focus of mastication occurred. In *Ysengrinia* the anterior premolars are very small, and the intact right P1–3 show virtually no wear (p1–3 are badly damaged), suggesting that P1–3/p1–3 were essentially nonfunctional. This lack of wear on anterior premolars contrasts with the pronounced wear on the upper and lower canines and I3. The canines and I3 of *Y. americana* exhibit strong wear facets indicative of a mature animal. The tips of upper and lower canines are blunted from heavy wear. Extensive wear surfaces on the mesial face of the upper canine and on the lateral face of I3 were produced by the insertion of the lower canine between these upper teeth. The lower canine has been so heavily abraded that it has been reduced to a rounded peg whose anterior and posterior wear surfaces penetrate the dentine. Similarly, the carnassials and molars show significant wear. However, the carnassial pair has maintained near-vertical shear surfaces, and m1 has a deep wear groove on the posterolabial surface of the trigonid that cuts 4–5 mm downward into the labial face of the talonid. This wear groove, cut by the tall M1 paracone, is particularly conspicuous. The tips of the major cusps of carnassials and molars show blunt wear, as does p4, but the degree of wear on these teeth is not as pronounced as would be expected given the condition of the canines and I3s. The dental wear pattern differs in this respect from that of *Daphoenodon superbus* in which wear on canines and I3 (relative to carnassials/molars) is much less pronounced (fig. 7). *Ysengrinia* apparently maintained more vertical shear planes on its carnassials for a longer interval during its lifespan than other contemporary amphicyonids such as *Daphoenodon* and *Amphicyon*.

Surprisingly, vertical carnassial shear is still evident in this aged adult *Y. americana* (F:AM 54147), and the carnassials and molars have not been worn to flat surfaces. As the North American amphicyonids *Daphoenodon* and *Amphicyon* age, their tooth wear patterns demonstrate that shearing occlusion of carnassials and molars gradually transforms to a more horizontal grinding-crushing mode. In older animals the vertical shear surfaces of the carnassials are entirely worn away, and in the oldest individuals the vertical planes of the molars (such as inner surfaces of paracone-metacone) are worn flat. Finally, molar occlusion in aged individuals

involves the apposition of flat subhorizontal surfaces, and the carnassials are low, blunt, rounded platforms effective only in crushing food material. It is of particular interest that the same wear progression occurs in living canids (*Canis lupus*, *C. latrans*, various foxes and jackals) for which Scapino's jaw mechanism utilizing a mobile symphysis can be inferred. Therefore, the evident dental and osteological similarities of the jaws shared by canids and early Neogene amphicyonids, such as *Y. americana* and *D. superbus*, argue for a pattern of mandibular occlusion like that described by Scapino for living canids. This pattern is documented by tooth form and number, mandibular morphology, including the anatomy of the mandibular symphysis, and by the ontogeny of tooth wear directly observable in rare population samples of beardogs such as *D. superbus*.

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APPENDIX 1

Letters from H.C. Clifford to O.C. Marsh in the Yale Peabody Museum establish the geographic location of Clifford's explorations during 1875. Clifford made several trips between March 13 and December 30, 1875, and on one of these must have collected the palate, an upper canine, and a calcaneum, later designated the holotype (YPM 10061) of ''*Amphicyon*'' *americanus* by Wortman (1901). The 1875 correspondence records only two occasions when Clifford was likely to have collected the amphicyonid: in March during his initial trip to the head of the White River, or on a second visit in late May–early June. Other documentation in the YPM archives indicates that YPM 10061 was collected during Clifford's first trip in March 1875, very likely at the same time and at the same locality as Marsh's holotypes of the chalicothere *Moropus elatus*.

In March 1875, Clifford reported the discovery and partial excavation of a brontothere skull (YPM 12048) and fossils of ''small animals'' in the Chadron Formation along the White River near the Spotted Tail Agency (letter to O.C. Marsh, March 13, 1875, YPM archive). He eventually traveled south from the White River badlands and the agency, crossing the Niobrara River, to ship the fossils from Sydney, Nebraska, on April 2. A letter written by Yale paleontologist R.S. Lull to W.J. Holland on November 6, 1908, establishes that the type material of *Moropus elatus* was collected on March 24, 1875, ''*en route* from Crow Buttes to Sydney, presumably where the trail crosses the Niobrara River'' (Holland and Peterson, 1914: 225).

Although Lull and Holland believed that the trail to Sydney crossed the Niobrara River near the Agate fossil quarries, it in fact intersected the river much farther east, just a few miles west of Marsland, Nebraska. The discovery by Harold Cook of an early excavation and dump, overgrown by vegetation, not far from the river crossing caused W.D. Matthew to accept the site as Clifford's probable source for the types of *M. elatus* (Matthew, 1929: 520).

The types of *Moropus elatus* are foot bones and a patella cataloged as YPM 13081, 24631, and 24632. These elements also bear the YPM accession number 704. This accession number appears at the head of the March 13, 1875, letter from Clifford to Marsh, indicating that the specimens collected on the March trip were accessioned under 704. Significantly, the holotype of ''*Amphi-*

cyon'' *americanus* Wortman is included in accession 704, demonstrating that it too was collected by Clifford during the March trip.

Both Ted Galusha of the Frick Laboratory and Margery Coombs of the University of Massachusetts have suggested that Clifford's excavation, as identified by Cook, corresponds to the site of the Morava Ranch Quarry of the American Museum, located ~6 miles (~9.6 km) west of Marsland, Nebraska. Galusha worked the site in 1940, as did Coombs in 1975 (Coombs and Coombs, 1997). Their excavations produced the remains of both *Moropus elatus* and *Ysengrinia americana*, including an edentulous mandible of the amphicyonid (F:AM 25423) which corresponds in size to Wortman's holotype palate. In addition, an M1 (F:AM 25420, Hunt, 1972: fig. 10A) collected by Galusha is virtually identical to the M1 of YPM 10061. These discoveries strengthen the assertion that Morava Ranch Quarry was a likely source of YPM 10061.

Is Morava Ranch Quarry the only site where YPM 10061 could have been collected? South of the Red Cloud and Spotted Tail agencies, the Pine Ridge escarpment is formed by Arikaree Group strata that Clifford would have traversed on his route to Sidney. The palate must have been collected from either upper Arikaree rocks of the escarpment or from upper Arikaree rocks in the valley of the Niobrara River immediately south of the escarpment. The preservation and color of the palate and teeth are similar to fossils from the Harrison Formation and lower part of the Upper Harrison beds, the principal upper Arikaree rock units in Sioux and Dawes Counties, Nebraska. Although the Yale drawer label states that the holotype was found by Clifford in ''L. Miocene (Arikaree), White River, Neb.'', this appears to be in error. The Yale catalogue records most specimens of accession 704 as ''White River, Nebraska'' because most of the fossils came from the White River badlands near the agencies. However, accession 704 also lists a few fossils collected in the Niobrara valley and supports Wortman's (1901) published statement that YPM 10061 came from the ''Loup Fork beds, Niobrara River, Nebraska''. Wortman's ''Niobrara River'' attribution suggests that he had some knowledge that YPM 10061 actually was found in the Niobrara valley where the Harrison Formation and Upper Harrison beds are fossiliferous. Although Clifford could have collected the amphicyonid as he traversed the Pine Ridge during his departure from the White River country, these upper Arikaree strata are not particularly fossiliferous, hence it is more likely that he found it a few miles farther south in the Niobrara valley. The term ''Arikaree'' was not applied to these strata until 1898–1899 when N.H. Darton of the United States Geological Survey mapped these rocks; prior to that time they would have been considered the ''Loup Fork'' beds as reported by Wortman.

APPENDIX 2

Viret's (1929) hypodigm of *gerandianus* included, in addition to the holotype mandibular fragment with p2–m1 (FSL 213828), a second nearly edentulous mandible with only m2 (MGL St.-G. 2848) and a tentatively referred rostrum with partial upper dentition (Muséum National d'Histoire Naturelle, Paris). Bonis (1973) noted that these three specimens are from different individuals. The teeth of FSL 213828 occlude reasonably well with the teeth of the rostrum, and thus assembled, the composite dentition indicates a carnivore somewhat smaller than *Y. americana*. If the holotype lower dentition of *Y. gerandiana* and the rostrum are correctly placed in the same species, then this smaller amphicyonid is unknown in North America; North American *Ysengrinia* shows closest affinity to *Y. tolosana* from Paulhiac (NMB Pa 951). In addition, there remains some uncertainty with regard to the m2 of *Y. gerandiana* because the holotype lacks this tooth, which is only retained in the referred mandible (MGL St.-G. 2848). The eventual discovery of a *Y. gerandiana* mandible that includes the complete premolar-molar toothrow with m2 is essential to confirm the identity of the lower dentition of the genus.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://library.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

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